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SMALL MAMMAL WINTER ABUNDANCE AND DISTRIBUTION IN THE CANADIAN MIXED GRASS PRAIRIES AND IMPLICATIONS FOR THE SWIFT FOX

by

ERIKA E. KLAUSZ

A thesis

submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **Master of Science**

DEPARTMENT OF RENEWABLE RESOURCES

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **SMALL MAMMAL WINTER ABUNDANCE AND DISTRIBUTION IN THE CANADIAN MIXED GRASS PRAIRIES AND IMPLICATIONS FOR THE SWIFT FOX** submitted by **ERIKA E. KLAUSZ** in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE**.

R. W. Wein

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J. O. Murie

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Date April 15, 1997

DEDICATION

I dedicate this thesis to the
Dearest Mom in the world
Who made so many sacrifices
So that I might give this a whirl

She instilled in me the value
Of nature's beauty and wonder
So that later on in life
I would pursue its mysteries and ponder

I hope my contribution
However small it may be
Will inspire all to appreciate nature
The way it was meant to be

So by conveying to the reader
There is still much work to be done
We should strive to find solutions
Before the problems are too far gone

By: Erika E. Klausz

ABSTRACT

The relationship of vegetation-snow-small mammal population demographics was investigated in swift fox (*Vulpes velox*) habitat along roadside ditches, coulees, and uplands in the mixed grass prairies of southern Alberta and Saskatchewan during early (November), mid (January-February), and late (March-April) winter of 1995-1996.

Mark-recapture methods of trapping resulted in a total of 163 small mammals in 9,360 trap-nights. Species diversity was low over the winter and deer mice (*Peromyscus maniculatus*) comprised 96.0% of the total catch, while shrews (*Sorex sp.*) constituted the remaining 4.0%.

Peromyscus populations were clumped over the winter and aggregation was noted. Deer mice did not reproduce from early November to early April. In spring, males travelled greater distances. Capture results were significantly different for study areas, habitat types, winter period, for area x winter interaction, and area x habitat interaction ($p<0.05$). *P. maniculatus* were more common in uplands in early winter, but in late winter, were more abundant in linear (roadside and coulee) habitats. Early winter trapping resulted in highest abundance values while there was a significant decline in small mammal abundance and biomass from early to late winter ($p<0.05$), except in one study area, where spring-like conditions were earlier and range conditions appeared to be better than for the other study areas.

Small mammals were considered important in the swift fox (*Vulpes velox*) winter diet, and their abundance and distribution likely influenced the winter survival of this endangered predator. From the study results, late winter appeared to be the most critical

time for swift fox survival when food was the most limited and foxes potentially had depleted fat reserves from the long winter.

Consequently, when releasing swift fox for reintroduction, factors such as the availability of food prior to release should be considered to optimize survival and the potential for a successful reintroduction.

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INTRODUCTION

Historical Range of the Swift Fox:

The historical range of the swift fox *(Vulpes velox)* in Canada extended in Alberta north to the 53rd parallel and west to the edge of the Rocky Mountains. In Saskatchewan, the population reached to the North Saskatchewan River. There is some speculation that populations once existed in the southwestern region of Manitoba, but this is uncertain (Carbyn *et al.* 1994). The last documented swift fox record in Canada was in 1938 near Manyberries, Alberta (Soper 1964).

Suitable Habitats:

Studies have shown that agricultural fields in northern areas may be poor swift fox habitat because of the lack of suitable denning sites, an insufficient prey base due to disturbance factors, and the use of pesticides and rodenticides (Carbyn *et al.* 1994). River valleys, coulees, and brushy areas are not favoured for denning (Mamo 1994); however, this does not imply that these are not important hunting areas for the fox. The most suitable habitat appears to be native grasslands with short grass cover and flat to slightly rolling topography (Mamo 1994). Vegetation structure can vary considerably within the Canadian mixed grass prairies depending on habitat. Roadside ditches and coulee habitats with abundant vegetation are a very small percentage of the landscape but may well prove to be important sites for small mammal prey. Close proximity to roads provide suitable hunting grounds for swift fox (Hines and Case 1991).

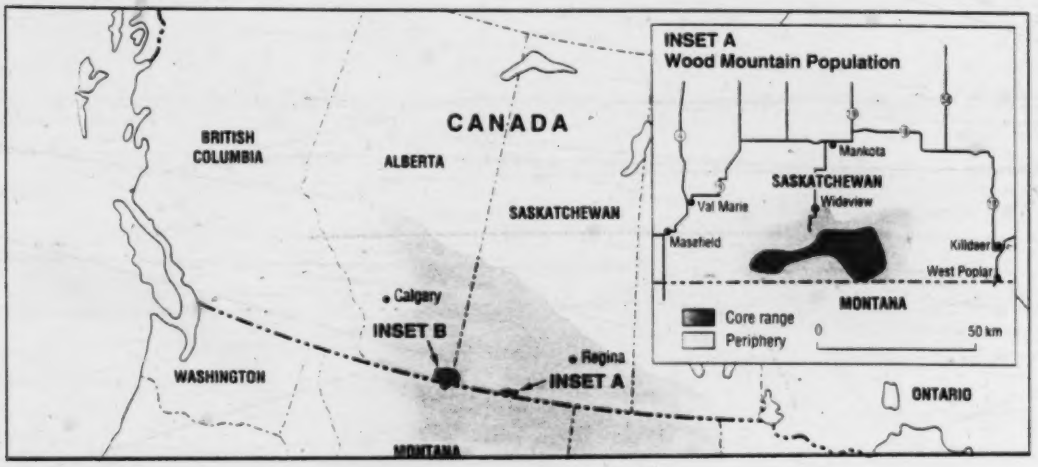
Present Range and Numbers:

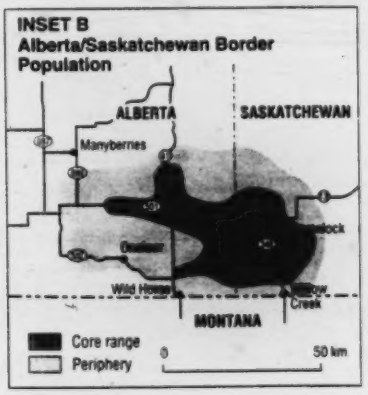
Highest known population densities of swift fox are found in two areas including Wood Mountain, Saskatchewan and the Alberta/Saskatchewan Border region (Fig. 1). Since the initiation of efforts to reintroduce the swift fox to the Canadian prairies from 1983 - 1996, 888 captive-raised and wild-caught swift foxes have been released. Numbers are currently estimated to be around 289 foxes in southern Alberta and Saskatchewan (Cotterill and Moehrenschlager 1997). The viability of the current population is not known, and there are still many unanswered questions as to the exact factors that may limit the population's long-term survival. The present study is hoped to shed some light on the subject.

Objectives:

The objective of this study was to test the hypothesis that because swift foxes were at the northern limit of their range in the Canadian prairies, winter small mammal prey were potentially limiting in the winter. The purpose of the study was to assess the relative abundance, biomass, and distribution of small mammals in three different prairie habitat types. Vegetation structure, ground cover, and snow depth within each habitat type were quantified to determine how these factors influenced distribution and abundance of small mammals throughout the winter and what this implied for the swift fox.

Figure 1: Present swift fox range and location of study areas in the Canadian mixed grass prairies - Grasslands (Val-Marie), Onefour, and the Border (Willow Creek/Govenlock).





Background:

A combination of environmental and anthropogenic factors contributed to the eventual extirpation of the swift fox from the Canadian prairies. In the past 200 years, the Canadian prairies have changed dramatically. Today, only 24% of the original 24 million hectares of native mixed-grass prairies in Canada remain (Trottier 1992). With the arrival of settlers; the expansion of agriculture, habitat destruction, disease, trapping, inadvertent killing of foxes during predator control programs (Hines 1980; Carbyn *et al.* 1994), the extinction of the plains bison (*Bison bison*), plains grizzly (*Ursus arctos horribilis*), and plains wolf (*Canis lupus nubilus*) have all contributed to a highly altered ecosystem. In more recent years; rodenticide and pesticide use, an increased coyote population, and vehicular traffic have been responsible for high swift fox mortality.

Efforts have been made to preserve some of the remaining native mixed-grass prairies in Grasslands National Park, near Val Marie, Saskatchewan and a portion of the Suffield Military Base near Medicine Hat, Alberta. It is hoped that reintroduction of native species such as the swift fox will help sustain biodiversity and the health of the prairie ecosystem. The potential success or failure of a reintroduction depends on various biophysical factors, but food and habitat play key roles (RENEW 1994; Wallace *et al.* 1991). Declines in the primary prey base (mice) for kit foxes (*Vulpes macrotis mutica*) in southcentral California for example, contributed to poorer nutritional condition, lower reproductive success, high coyote-induced mortality, and hence a decline in fox numbers (White *et al.* 1996). Kit foxes retained preferences for small mammals and did not shift their diets to other prey even when small mammals were scarce (White *et al.* 1996).

Declines in rates of the staple food consumption appeared to have a strong influence on the population dynamics of this endangered fox.

In the northern extent of the swift fox range the availability of food becomes a lot more limited by late October as song birds migrate south, ground squirrels enter hibernation and insects and amphibians become dormant or die. Therefore, the diversity of food available to the swift fox during the winter is greatly reduced, and small mammals become an important source of prey (Hines and Case 1991). As a result, the Canadian Wildlife Service initiated this study to investigate the status of small mammals during the winter as part of the swift fox reintroduction effort. The objective was based on the observation that fall released foxes survived better than spring released foxes (Brechtel *et al.* 1993). This was attributed to two factors. Fall releases were all young of the year (5-6 months), while spring released foxes were one or more years old. The young foxes were released during their natural dispersing time when they established independence and were more apt to capture prey and avoid predators than older foxes that had been in captive conditions for a longer time. The second factor was prey abundance and availability. In the fall, grasshoppers were still available and easily accessible until the foxes established and familiarized themselves with their territories. As foxes gained hunting experience, the proportion of grasshoppers in scats decreased and small mammal remains increased (C. Mamo, pers. obs.). Swift fox population declines are also a concern in some of the northern States. The U.S. Report of the Swift Fox Conservation Team (1995) stressed the need to address factors potentially limiting swift fox (*Vulpes velox*) populations. The

report stated that "winter food resources may be particularly limiting in the northern portions of the swift fox range".

Small mammal populations reach their peaks in early winter (November) and then decline until spring when reproduction resumes (Beer and MacLeod 1966; Linduska 1950; Wolff 1989). In addition to prey abundance, swift fox survival likely depends on the availability of prey, which is probably limited by late winter freeze-thaw cycles and snow storms. Numerous small mammal studies in Canada and the United States have considered the relationship between vegetation cover and small mammal population dynamics (Birney *et al.* 1976; Grant and Morris 1971; LoBue and Darnell 1959; O'Farrell 1983; Rosenzweig and Winakur 1969; Rosenzweig 1973). Factors such as cattle grazing determine vegetation characteristics that will dominate in an area and consequently will influence the abundance and diversity of small mammal species. Under drought conditions, the effects of cattle grazing are even more pronounced (Branson 1985). Declines in small mammal populations during droughts result when plant production is poor and many species do not produce seeds, important in the diet of many granivorous species (Williams and Germano 1992). A decrease in prey diversity can be a consequence of overgrazing by cattle in a hot desert environment, which can lead to declines in kit fox density (O'Farrell 1983). During the winter, snow conditions interplay with vegetation characteristics to control small mammal population demographics. Therefore, in the winter it is important to know how closely small mammal populations are linked to both vegetation and snow conditions (Klausz *et al.* 1995).

The mark-recapture method of trapping is an effective way to provide information on habitat use, density, social habits, individual movements, sex and age ratios, home range, homing, and species diversity of small mammals (Baker 1968). Capture locations can reflect an animal's preferred living space or its foraging grounds (Baker 1968). Three different habitat types prevalent in swift fox range were selected for this study to determine which habitats were most desirable for small mammals over the winter. Each habitat exhibited differences in vegetation characteristics such as per cent cover, height, and litter depth. Upland habitats consisted of sparse and low vegetation, while coulee and roadside habitats had denser, higher vegetation. Measurements of vegetation characteristics within each habitat provided structural information and reflected the condition of that habitat under cattle grazing. Plants that increase or invade an area under increased grazing pressure because they are relatively tolerant of defoliation, or are less frequently grazed than other plants due to their less palatable nature (Vallentine 1990), such as sage brush, cacti, and club moss, are considered to indicate higher grazing intensity and poorer range condition (Smoliak *et al.* 1988). Different levels of grazing pressure result in widespread changes in vegetation altering aspects such as the structure, species composition, and biomass values (Johnston *et al.* 1971; Sims *et al.* 1978). It was predicted that areas with fewer increaser and invader species would have higher small mammal populations than regions that were more adversely affected by cattle grazing (Birney *et al.* 1976; Rosenzweig 1973; Rosenzweig and Winakur 1969).

Distribution and abundance of small mammals vary depending on habitat characteristics. *Peromyscus sp.* generally occupy a wide range of environmental conditions

(Baker 1968). Unlike *Microtus sp., Peromyscus* are largely nocturnal and movements are often in sparse vegetation not confined to runways with dense vegetation (Baker 1968). Voles prefer higher vegetation cover and show a lower decline in numbers over the winter when vegetation is more dense than populations with less vegetation cover (Taitt and Krebs 1983). Thus, small mammals were predicted to be affected differently by vegetation characteristics depending on species.

In addition to vegetation characteristics, snow conditions over the winter were considered important in influencing small mammal populations. During early winter in a boreal forest in Northern Russia when the snow was still shallow and temperatures did not fall below -5 to -10°C, small mammal population distribution and activity was not affected; voles, mice, shrews, and even moles were active on the snow surface (Formozov 1964).

In mid-winter, snow becomes increasingly deep and linear habitats (coulees and roadsides) have softer and less dense snow supported by higher vegetation (Coulianos and Johnels 1963) and are characterized by fairly constant temperatures and saturated air (Pruitt 1957). In upland regions, there is less snow with more crusting as these habitats are more exposed to the wind. As a result, upland habitats were predicted to be less abundant in small mammals as the winter progressed since places where the snow is blown away are avoided (Formozov 1964). Abundance, biomass, and survival of small mammals would be higher in the linear habitats than in the more exposed upland habitats. In years with above average snowfall small mammal populations were expected to be low. In Colorado, deer mouse populations were negatively correlated with depth of snow; populations were low in years of deep snowpack, and vice versa (Steinhoff 1976). As snow depth increases and

temperatures fall below -10°C , small mammals concentrate their activities under the snow and rarely come to the surface (Formozov 1964). During this time, availability of small mammals would probably be limited for swift fox, although *Peromyscus* species would likely be more available because they are more active above the snow than vole species (Halpin and Bissonette 1988). With snow depths of 10-15 cm, runways beneath the snow remain relatively stable and do not collapse. Subnivean nests constructed on the soil surface in the dead grassy cover protect small mammals from low temperatures because of the lower conductivity of snow than frozen soil (Formozov 1964).

By late winter when the snow begins to melt, habitats with more snow-free zones and less standing water would be selected by small mammals. Coulees carry snow melt run-off and may flood in some regions, but southern exposed slopes are the first to experience snow melt where it is drier and temperatures are warmer. Roadsides probably experience similar conditions to coulee habitats. Overall, a steady decline in small mammal numbers from early to late winter is predicted in all areas and habitats as a result of natural mortality and the cessation of breeding (Krebs and Wingate 1985; Linzey and Kesner 1991; Metzgar 1979; Wolff and Durr 1986), which would implicate late winter as the most crucial for swift fox survival.

STUDY AREAS

Study areas were located in present swift fox range in the native mixed-grass prairies of southern Saskatchewan and Alberta (Figure 1): the "Onefour" Grazing Research Substation in SE Alberta (49° 05'N, 110° 30'W); the Alberta/Montana/Saskatchewan "Border" region near Consul, Saskatchewan on the Govenlock Community Pasture (49° 02'N, 110° 50'W), 75 km east of Onefour; the Dixon Provincial Community Pasture surrounding the West Block of "Grasslands" National Park near Val Marie, Saskatchewan (49°14'N, 107°44'W), 250 km east of the Border region. Cattle in these regions were grazed on a rotational basis from May to October. Mean monthly winter climatic normals for the study areas, where information was available, are shown in Table 1. Weather data were available for the winter trapping period of the present study (1995-1996) for Grasslands and Onefour (Appendix 2).

The area trapped (including distances between replications) at Onefour encompassed a region of about 35 km^2 (Figure 2). The Border region encompassed an area of about 50 km^2 (Figure 3). The Grasslands study area encompassed a trapping area of 100 km^2 (Figure 4).

Table 1: Selected mean climatic normals for the winter months near the three study areas, Val-Marie (Grasslands), Manyberries (Onefour), Consul (Border). Adapted from Canadian Climatic Normals, 1961-1990, Environment Canada.

Measurement	Station	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Monthly mean temperature (°C)	Val-Marie	5	---	---	-13	---	-4	4
	Manyberries	6	-3	-9	-11	-8	-3	5
Snowfall (cm)	Val-Marie	6	12	15	19	12	15	7
	Manyberries	6	14	22	24	18	21	18
	Consul	4	9	14	19	12	11	9
Extreme daily snowfall (cm)	Val-Marie	18	19	14	15	18	31	46
	Manyberries	20	29	16	22	39	41	42
	Consul	24	24	13	25	16	20	24
Wind (km/hr)	Suffield	19	18	18	18	18	18	19
	Manyberries	---	18	19	---	19	19	21
	Manyberries	77	76	92	85	95	89	85
Extreme minimum temperature (°C)	Val-Marie	-25	-37	-47	-49	-48	-41	-28
	Manyberries	-24	-35	-41	-43	-43	-36	-26
	Consul	-21	-33	-48	-47	-41	-34	-27
Daily maximum temperature (°C)	Val-Marie	13	3	-5	-6	-4	3	12
	Manyberries	13	3	-4	-6	-2	3	12
Mean annual snowfall (cm)	Val-Marie	91						
	Manyberries	128						
	Consul	82						

Figure 2: Location of trapping transects for the Onefour study area.

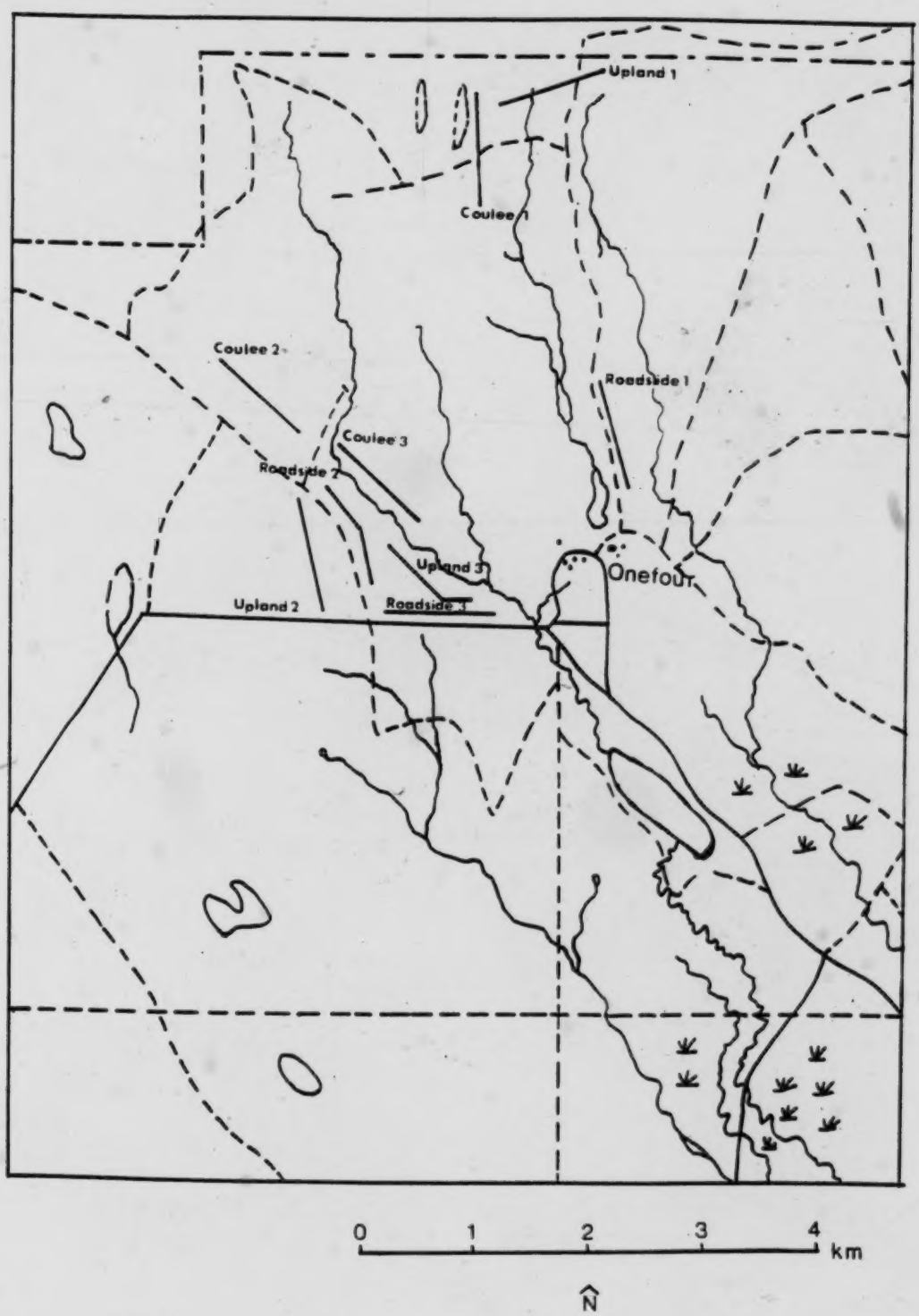


Figure 3: Location of trapping transects for the Border study area.

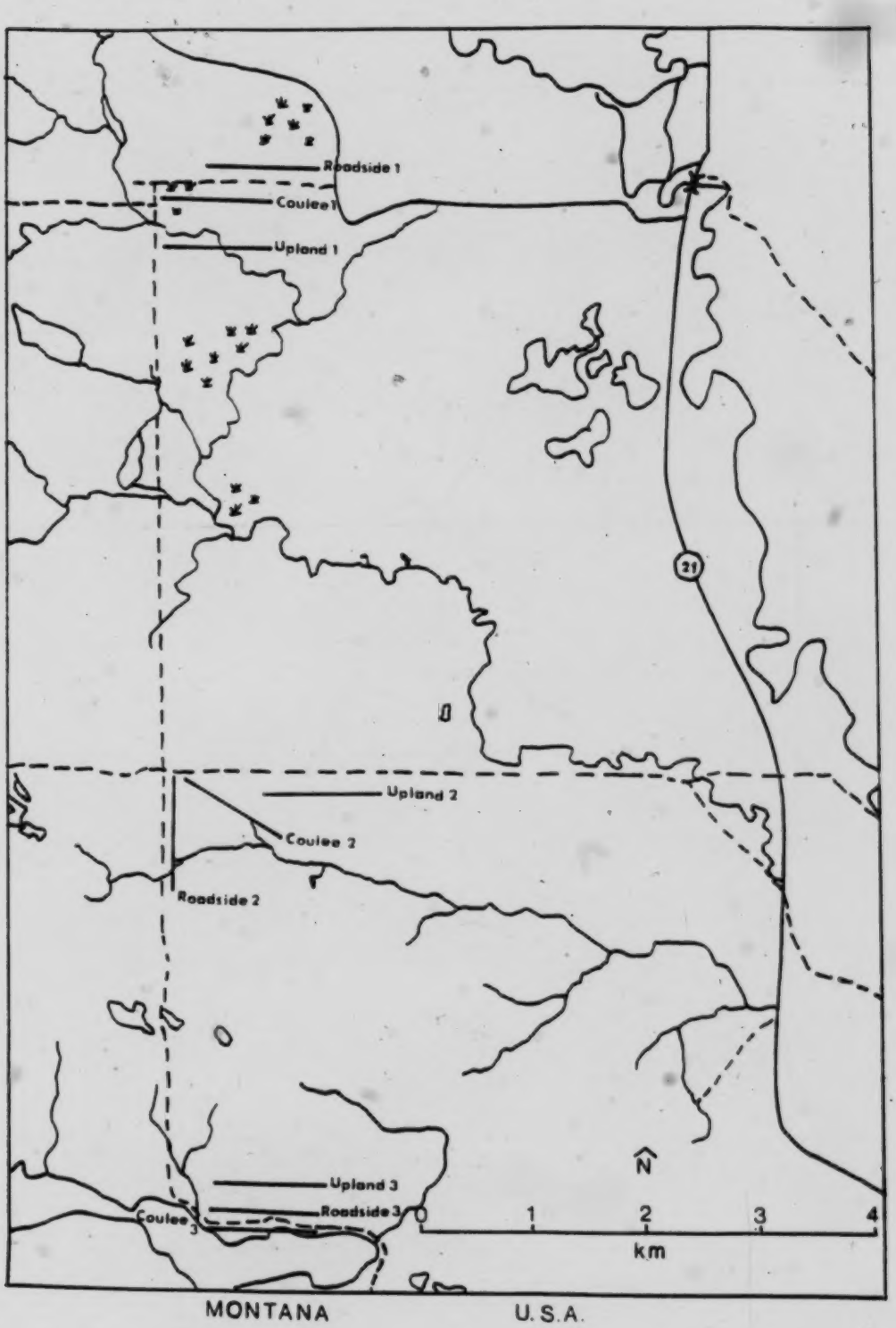
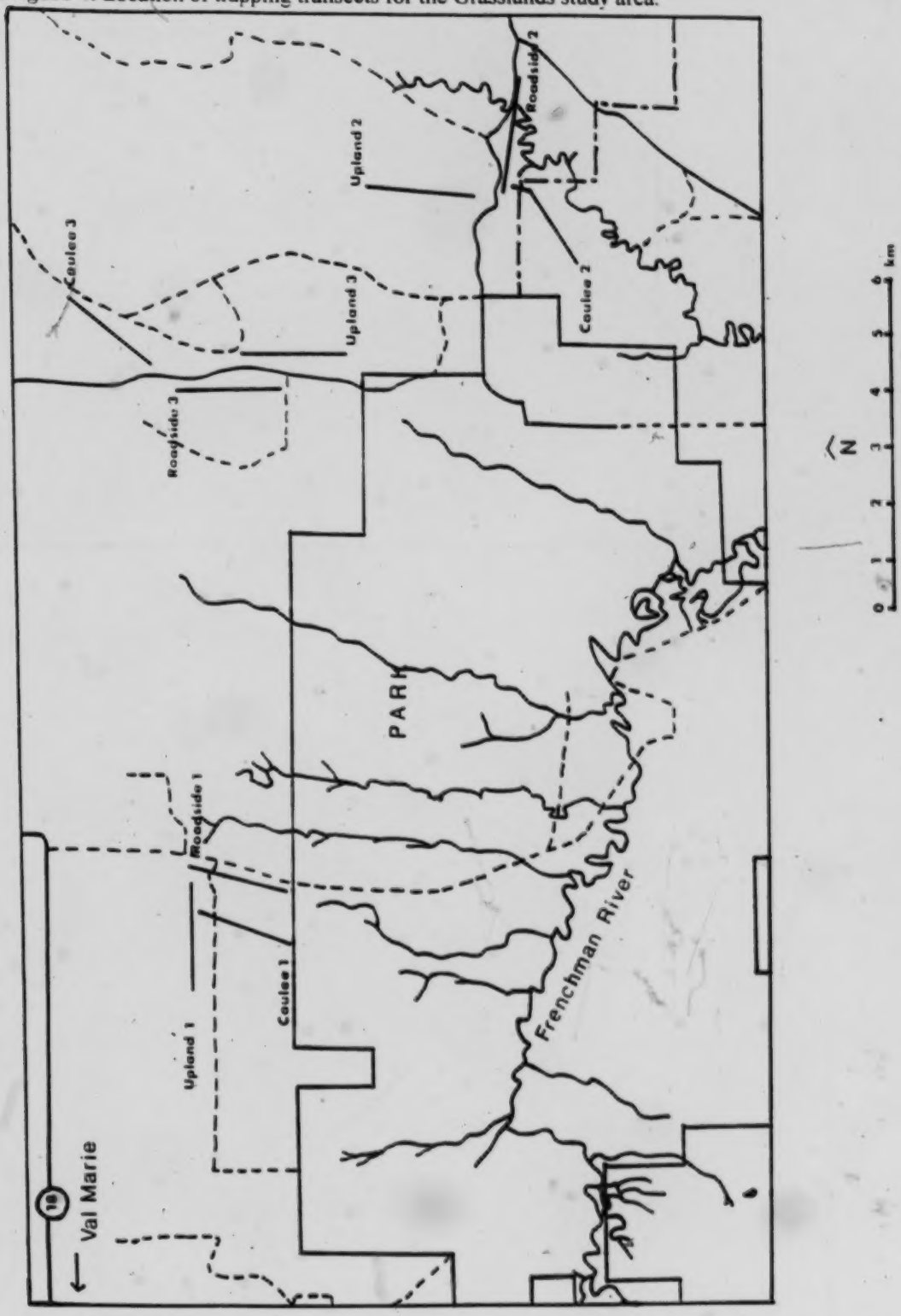


Figure 4: Location of trapping transects for the Grasslands study area.



Replicates of grazed upland areas and adjacent linear coulee and roadside habitats were no greater than 5 km from adjacent study sites. Upland habitat was flat to gently rolling, with the vegetation low and sparse, characterized by mid and short grasses, many forbs, and few shrubs (Looman 1980). The most common vegetation types were the *Stipa-Bouteloua-Agropyron* association found in the loamy Brown Soil Zone consisting mostly of the needle and thread, blue grama, and northern and western wheatgrasses (Smoliak 1985). June grass (*Koeleria cristata*), Sandberg's bluegrass (*Poa sandbergii*), and prickly-pear cactus (*Opuntia polyacantha*) were also present. Forbs included moss phlox (*Phlox hoodii*), broomweed (*Gutierrezia sarothrae*), golden aster (*Chrysopsis villosa*), and little club moss (*Selaginella densa*). Shrubs were pasture sage (*Artemisia frigida*), winterfat (*Eurotia lanata*), and sagebrush (*Artemisia cana*). Coulee habitat was characterized by gentle to steep-walled valleys, which carried runoff after heavy rains or during snow melt and widths varied from 2 to 12 meters across; the vegetation was often diverse and dense (Willock 1990). Coulee habitats exhibited taller vegetation and denser shrub/forb cover than uplands, with wild rose bushes (*Rosa acicularis*), wild mustard (*Sinapis arvensis L.*), wild licorice (*Glycyrrhiza lepidota*), sagebrush, and golden aster. Roadside habitats were ditches between fence and vehicle tracks no more than 5 meters in width. Often, the vegetation was tall and primarily crested wheat grass (*Agropyron cristatum*) with patches of bare ground.

METHODS

Trapping Procedures:

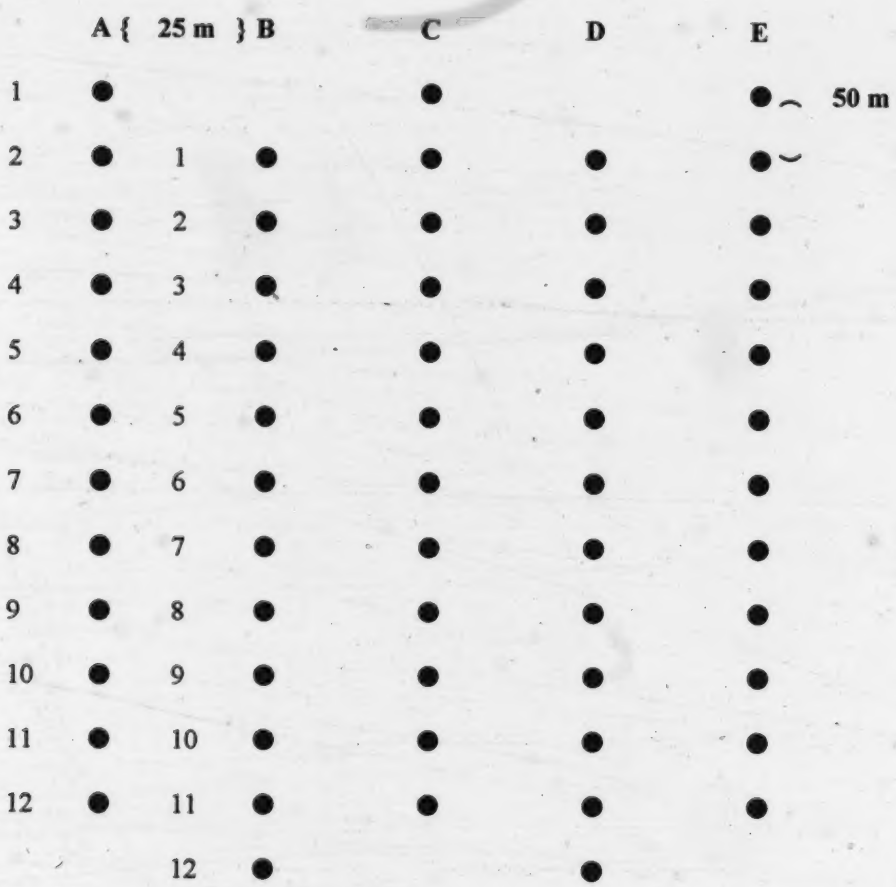
Data were collected in three study areas to account for potential winter snow variability between regions and relate it to differences in small mammal populations. Trapping was conducted by two people per trap session. Precautionary measures were taken for the HANTA virus by wearing latex gloves and HEPA filter masks when cleaning traps. In the field, when temperatures were too cold to use latex gloves and masks, tight fitting woolen gloves were worn while facing down-wind. Gloves were bleached each night to be reused the following day.

Small mammals were live trapped during early winter (November), mid-winter (January-February), and late winter (March-April) of 1995-1996 (Table 2). In early winter, upland habitats were trapped on grids consisting of 60 traps, with 5 rows spaced at 25 meters, and each row containing 12 traps spaced at 50 meter intervals staggered in a zig-zag fashion, covering a total area of 6 ha (Figure 5). Transects replaced grid trapping in mid and late winter and were set in the same area that grids occupied during early winter trapping. Coulee habitats were trapped along transects in all three winter periods. Roadsides were included at Onefour during early winter, and added to all three study areas in mid and late winter. Transects in each habitat type in each study area consisted of thirty traps set along a line spaced at 30 m intervals (Figures 2, 3, 4). Trap line census was considered an efficient method to provide relative abundance figures for comparison of populations of different areas or, of the same area at different

Table 2: Trapping schedule for early (November), mid (January-February) and late winter (March-April) for the three study areas; Onefour, Grasslands and Border.

Study Area	Winter Period	Trap Dates (1995-1996)
Onefour	Early	1 November - 8 November
Border	Early	14 November - 18 November
Grasslands	Early	23 November - 27 November
Onefour	Mid	17 January - 22 January
Border	Mid	24 January - 31 January
Grasslands	Mid	3 February - 7 February
Onefour	Late	16 March - 21 March
Grasslands	Late	24 March - 31 March
Border	Late	1 April - 6 April

Figure 5: Configuration of grid trapping in upland habitats in early winter.



times (Hansson 1969; Petticrew and Sadleir 1970; Stickel 1948), especially for linear habitats such as coulees and roadsides. Each trapping session in a study area was operated for four consecutive nights and consisted of a total of 270 traps providing 1080 trap nights of effort per trap session in each study area. The only exceptions to this were at Onefour during early winter where 1440 trap-nights of effort was expended, and at Grasslands during mid-winter where trap effort was 360 trap-nights. The majority of resident mice were assumed to be caught by the fourth day of trapping (Seber 1982). Trap positions were marked with fluorescent numbered pin flags and remained the same from one winter period to the next. A 7 day rotation was required to complete each trapping session in each study area.

Longworth traps were used in the live capture of animals because of their compact nature (chamber measured $14^1/_2$ cm x $6^1/_2$ cm, entrance measured 3 cm high x $4^1/_2$ cm wide) and because the chamber was completely sealed, the only space occurred between the entrance-chamber connection. Prior to each trapping session, traps were baited with a peanut butter-oat mixture and provided with fibrefill for bedding. Each trap was wrapped with bubblewrap ($3^1/_{16}$" bubble size), to provide insulation, and secured with duct tape and elastic bands. Traps were placed on the ground surface and, in deep snow (>10cm), were covered with cardboard lids and then with snow. In this way, a subnivean space was created so snow would not block the entrance-way and small mammals could access the traps through their tunnels.

Traps were set in the day and checked the following morning for animals, trap mechanism sensitivity, and presence of ample bait and bedding. Date and location of

captures were recorded. Sex, species, weight; measured to the nearest 0.1 g with a 50.0 gram Pesola spring scale, and reproductive condition was determined; testes abdominal or scrotal if a male, nipples visible (lactating or not), pregnant if presence of embryos, and vagina perforate or non-perforate if a female. Animals were checked for recapture status and new individuals were ear-tagged with individually numbered metal tags and released. Individuals were classified as sub-adults or adults based on size and colour of pelage. Sub-adults weighed ≤15.0g with grey guard hairs and no apparent beige undertones. Adults weighed >15.0g with distinct beige/brown pelage (Fairbairn 1977[a]).

Estimation of Population Size:

The program "CAPTURE" was used to estimate small mammal population size by means of the mark-recapture method where a closed population was assumed (Otis *et al.* 1978). A closed population is defined as a population which remains unchanged during the period of investigation i.e.; the effects of migration, mortality and recruitment are negligible (Seber 1982). Small mammal population estimates were assumed to represent indices of relative abundance of rodents (Windberg and Mitchell 1990) and were subsequently used for statistical analysis. The program CAPTURE bases its population size estimates on tests of various underlying assumptions and thereby chooses one of the 8 models that best fit the pattern of small mammal capture data: M(o), M(h), M(b), M(bh), M(t), M(ht), M(bt), or M(tbh). The model considers three distinct sources of variation (and the combination of these factors) acting on capture probabilities: 1. variation over time, M(t) 2. behavioural variation as a result of first capture (trap response), M(b), and 3.

variation over individuals (heterogeneity), M(h). Additionally, the "null" case (Model M(o)) is considered in which capture probability is constant with respect to all other factors (Otis *et. al.* 1978). In instances where the model chosen for best estimates were M(th), M(tb), or M(tbh), there were no theoretically appropriate estimators for population size and therefore, the next best fitting model for which an estimator existed was selected. If this was not appropriate then the total capture for that area was taken as the best estimate for population size.

Catch Effort and Biomass Estimates:

Catch/effort (CE), expresses the number of small mammals caught relative to trapping effort (Nelson and Clark 1973; Sharpe and Millar 1991). This measurement is especially useful when different trapping protocols are used. Trap success is converted to 100 trap nights of effort and can be considered to be an index of density (Fleharty and Navo 1983) where a higher C/E rate likely relates to a greater density of animals. The equation adapted from Nelson and Clark (1973) is :

$$CE=100A/N$$

Where A is the number of animals of each species caught and N is the number of trap nights. Sprung traps occurred rarely and were ignored in the calculation.

Biomass index values were calculated by the number of animals caught per trapping session (4 days) multiplied by the mean weight of small mammals on a given plot

(g/plot) in order to determine the available food on a weight basis for the swift fox. Biomass values for early winter in upland regions were calculated on a g/ha basis, while the rest of the biomass values represented g/km of transect.

Movements and Distribution:

Range length is the measure of the distance between the most widely separated capture points (DeBlase and Martin 1981). This can be used to estimate movement and distribution of individuals. Further, distribution of animals in an area can be categorized as random, uniform, or clumped (DeBlase and Martin 1981). One can test for the type of dispersion pattern present by using an index of dispersion (I_s) (Morisita 1962) where:

$$I_s = N \frac{\sum ni(ni-1)}{\sum x(\sum x-1)}$$

N equals the total number of observations, ni equals the number of animals observed in the ith observation, and $\sum x$ equals the total number of animals found in all observations. Randomness in dispersion is indicated by a value of one while values less than or greater than one indicate, respectively, that the distribution is uniform or clumped.

Habitat Measurements:

Ground cover was assessed in each habitat type during snow-free periods in November and April. Percent cover by shrub, grass, forb, cactus, moss, lichen, stone, cattle dung, and bare ground was estimated visually within a 1 m^2 gridded quadrat at every third trap station (10 measurements/site). Vegetation height and litter depth were measured from the ground surface at five random points within the gridded quadrat during each assessment of ground cover.

Snow depth measurements were taken around each trap station (10-20 cm) at the time of trapping.

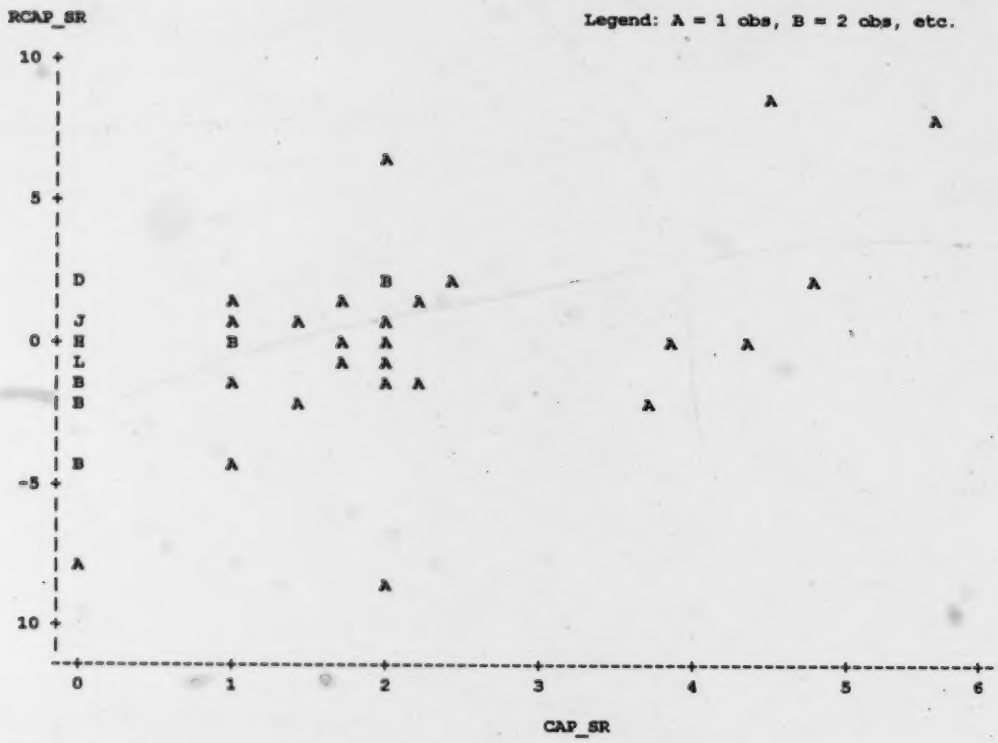
Statistical Analysis:

Analysis of Variance (ANOVA) and General Linear Models (GLM) procedures were used to test for significant differences of small mammal population size (after estimates of the program "CAPTURE"), between study areas, habitats, between winter sessions, the interaction of these main effects, and for multiple comparison of least square means. Since sample sizes were quite small, the above statistical procedures were selected since they were quite robust to the normality assumption (Dr. R. T. Hardin, pers. comm.). To test normality of data points graphically, a distribution of residuals against the square root transformation of capture data were plotted; points distributed randomly in a fairly straight line indicate normality (Figure 6). The square root transformation was done to stabilize the variation incurred by small sample sizes to better fit the linear model of the Analysis of Variance procedure (Box *et al.* 1978; Dr. R. T. Hardin, pers. comm.).

The 2-way analysis of variance procedure and the general linear models procedure were used to detect significant differences in percent ground cover, standing height of vegetation, and litter depth between study areas and habitat types. Snow was used as a dependent variable to test for significant differences between areas, habitats, time in winter, and the interaction of these main effects. GLM was used for multiple pair-wise comparison of least square means to help detect where significant differences occurred within study areas, habitats, winter periods, and the interaction of these.

Significant levels were reported as: $p<0.10$, moderately significant; $p<0.05$, significant; $p<0.01$, highly significant (Schlotzhauer and Littell 1987).

Figure 6: Plot of residuals against square root transformation of capture.



NOTE: 12 obs had missing values.

RESULTS

Small Mammal Demographics:

Trapping over the winter (November - April) resulted in a total capture of 163 small mammals of which 157 were *Peromyscus maniculatus* (Table 3) and the remaining 6 were *Sorex sp.* Shrew species were not identified with certainty (teeth were not examined under a microscope) but, by visual observation were thought to be either prairie shrew (*Sorex haydeni*) or dusky shrew (*Sorex monticolus*). Overall trap mortality of *P.maniculatus* was 3.8%, a low value considering the cold temperatures and high wind speeds. Trap mortality of shrews was 100%.

Capture of *P. maniculatus* varied significantly (note: when referring to "capture" of *P. maniculatus,* I refer to the estimation of numbers after analysis with the program "CAPTURE", unless otherwise stated) when the data were transformed with the square root procedure, with study areas ($p<0.001$), winter periods ($p<0.001$), habitats ($p<0.05$), for area x habitat ($p<0.05$), and area x winter period interactions ($p<0.001$)(Table 4). Study areas and winter periods were the most important source of variation in captures. Without transformation, habitat was moderately significant ($p<0.1$) (Schlotzhauer and Littell 1987). Results for catch effort (C/E) (Table 5) were the same as for "capture" under the analysis of variance procedure. Multiple comparison of least square means for pair-wise comparisons under the square root transformation of capture data (Table 6), showed significant differences between the Border and Grasslands ($p<0.05$), and between Grasslands and Onefour study areas ($p<0.05$).

Table 3: Total winter captures of *Peromyscus maniculatus* in three study areas (Grasslands, Border, Onefour) in three habitats (upland, coulee, roadside). Estimates of population size by the program CAPTURE are in parentheses.

Study Areas	Winter Session	Habitat Types			
		Upland	Coulee	Roadside	TOTAL
Grasslands	Early	53 (56)	34 (50)	---	87 (106)
	Mid	2 (4)	2 (4)	1 (1)	5 (9)
	Late	1 (1)	4 (4)	1 (1)	6 (6)
	TOTAL	56 (61)	40 (58)	2 (2)	98 (121)
Border	Early	24 (26)	10 (11)	---	34 (37)
	Mid	0	0	0	0
	Late	0	3 (5)	0	3 (5)
	TOTAL	24 (26)	13 (16)	0	37 (42)
Onefour	Early	0	0	2 (3)	2 (3)
	Mid	0	0	1 (1)	1 (1)
	Late	2 (2)	7 (9)	10 (11)	19 (22)
	TOTAL	2 (2)	7 (9)	13 (15)	22 (26)
	GRAND TOT.	82 (89)	60 (83)	15 (17)	157 (189)

Table 4: Analysis of variance procedure for population estimates of *P. maniculatus* and under square root transformation of capture, for study areas, habitats, winter sessions, and the interaction of these main effects.

Dependent Variable: CAPTURE

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	42	2008.99482402	47.83321010	3.11	0.0015
Error	26	400.30952381	15.39652015		
Corrected Total	68	2409.30434783			

R-Square	C.V.	Root MSE	CAPTURE Mean
0.833849	143.2513	3.92383997	2.73913043

Source	DF	Anova SS	Mean Square	F Value	Pr > F
REP(AREA*HABITAT)	18	263.02380952	14.61243386	0.95	0.5369
WINTER	2	542.44720497	271.22360248	17.62	0.0001***
AREA*WINTER	4	735.12686911	183.78171728	11.94	0.0001***
HABITAT*WINTER	4	71.64068141	17.91017035	1.16	0.3497
AREA*HABITAT*WINTER	6	0.00000000	0.00000000	0.00	1.0000

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	394.23027375	197.11513688	13.49	0.0003***
HABITAT	2	89.91487414	44.95743707	3.08	0.0709*
AREA*HABITAT	4	149.30205708	37.32551427	2.55	0.0745*

Dependent Variable: CAP_SR

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	42	111.13100297	2.64597626	3.63	0.0004
Error	26	18.95941997	0.72920846		
Corrected Total	68	130.09042294			

R-Square	C.V.	Root MSE	CAP_SR Mean
0.854260	92.41819	0.85393704	0.92399242

Source	DF	Anova SS	Mean Square	F Value	Pr > F
REP(AREA*HABITAT)	18	7.74347837	0.43019324	0.59	0.8753
WINTER	2	29.46813802	14.73406901	20.21	0.0001***
AREA*WINTER	4	44.72199847	11.18049962	15.33	0.0001***
HABITAT*WINTER	4	5.24420453	1.31105113	1.80	0.1596
AREA*HABITAT*WINTER	6	0.00000000	0.00000000	0.00	1.0000

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	21.33120202	10.66560101	24.79	0.0001***
HABITAT	2	3.96009612	1.98004806	4.60	0.0243**
AREA*HABITAT	4	12.00394706	3.00098676	6.98	0.0014***

Significant for: * p<0.1, ** p<0.05, *** p<0.01

Table 5: Analysis of variance procedure for catch/effort of mice for study areas, habitats, winter period, and the interaction of these main effects.

Dependent Variable: CE

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	36	887.23066394	24.64529622	5.85	0.0001
Error	32	134.91484331	4.21608885		
Corrected Total	68	1022.14550725			

R-Square	C.V.	Root MSE	CE Mean
0.868008	115.2795	2.05331168	1.78115942

Source	DF	Anova SS	Mean Square	F Value	Pr > F
REP(AREA*HABITAT)	18	135.67658730	7.53758818	1.79	0.0738
WINTER	2	175.02190936	87.51095468	20.76	0.0001***
AREA*WINTER	4	281.61105360	70.40276340	16.70	0.0001***
HABITAT*WINTER	4	17.79052706	4.44763177	1.05	0.3947

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	153.63809984	76.81904992	10.19	0.0011***
HABITAT	2	45.12799146	22.56399573	2.99	0.0755*
AREA*HABITAT	4	78.36449532	19.59112383	2.60	0.0710*

Significant for: * p<0.1, ** p<0.05, *** p<0.01

Table 6: Multiple comparison of least square means for capture data and square root transformation of capture for the main effects of study areas, habitat types, and winter periods.

Standard Errors and Probabilities calculated using the Type III MS for REP(AREA*HABITAT) as an error term

AREA	CAPTURE LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	2.18518519	0.83154374	0.0171	1	.	0.0009***	0.2698
GRS	7.38310185	1.11950002	0.0001	2	0.0009***	.	0.0001***
ONFR	0.96296296	0.67895262	0.1732	3	0.2698	0.0001***	.

AREA	CAP_SR LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	0.82282336	0.14722710	0.0001	1	.	0.0002***	0.1258
GRS	1.91986321	0.19821055	0.0001	2	0.0002***	.	0.0001***
ONFR	0.51770691	0.12021042	0.0004	3	0.1258	0.0001***	.

HABITAT	CAPTURE LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	3.65866402	0.74780251	0.0001	1	.	0.7655	0.9817
RD	3.23773148	1.18290162	0.0135	2	0.7655	.	0.7783
UPLD	3.63485450	0.74780251	0.0001	3	0.9817	0.7783	.

HABITAT	CAP_SR LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	1.17039605	0.13240048	0.0001	1	.	0.6221	0.4923
RD	1.04699749	0.20943597	0.0001	2	0.6221	.	0.9872
UPLD	1.04299993	0.13240048	0.0001	3	0.4923	0.9872	.

WINTER	CAPTURE LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: i/j	LSMEAN(i)=LSMEAN(j) 1	2	3
EAR	7.78958333	1.08817912	0.0001	1	.	0.0001***	0.0004***
LATE	1.22222222	0.67895262	0.0886	2	0.0001*	.	0.8065
MID	1.51944444	0.98389582	0.1399	3	0.0004*	0.8065	.

WINTER	CAP_SR LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: i/j	LSMEAN(i)=LSMEAN(j) 1	2	3
EAR	2.06446215	0.19266510	0.0001	1	.	0.0001***	0.0001***
LATE	0.67577910	0.12021042	0.0001	2	0.0001*	.	0.4716
MID	0.52015223	0.17420145	0.0079	3	0.0001*	0.4716	.

Significant at: * p<0.1, ** p<0.05, *** p<0.01

Study Areas:

BRD=Border
GRS=Grasslands
ONFR=Onefour

Habitats:

CUL=Coulee
RD=Roadside
UPLD=Upland

Winter Session:

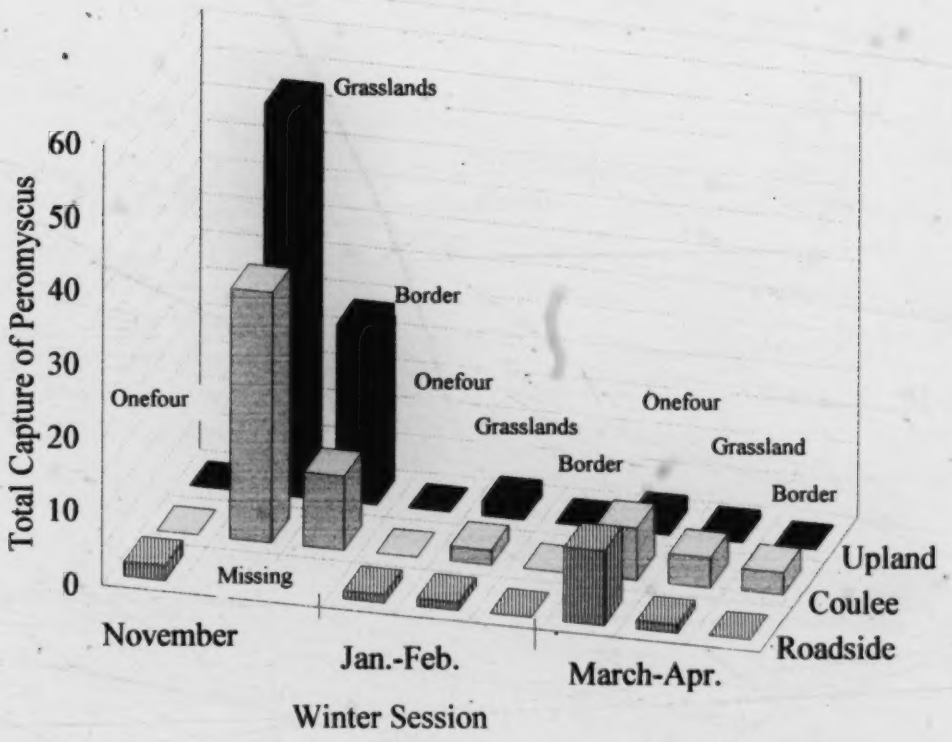
EAR=early winter
LATE=late winter
MID=mid winter

Differences were not significant ($p>0.05$) between the Border and Onefour. Least square means of capture indicated highest values for Grasslands followed by the Border and Onefour. Significant differences in capture occurred between early and late winter, and between early and mid winter ($p<0.05$). Highest least square mean values for capture occurred in early winter followed by late and mid winter, which were not significantly different from each other. Figure 7 summarizes the variation of distribution and abundance of *P. maniculatus* among habitats and winter periods.

Capture rates were indicative of low population densities throughout the winter. Capture success rates averaged over the three study areas were: 3.78% in early winter, 0.49% in mid-winter, and 0.87% in late winter. Densities calculated for upland regions (highest abundance values, except at Onefour) in early winter were 0/ha at Onefour, 3.0/ha at Grasslands, and 1.3/ha at the Border. The percent decline of *P. maniculatus* from early to late winter as indicated by total captures was a 93% decrease (81/87) at Grasslands, a 91% decrease (31/34) at the Border, and an 89% increase (17/19) at Onefour (Table 3). In late winter, numbers trapped at the Border and Grasslands were low and approximately the same. By mid-winter, there was already a major decline from numbers trapped in early winter (Table 3).

Recapture rates from early to mid to late winter were very low; only three male individuals in total were recaptured between winter trapping sessions. One male from Grasslands coulee habitat was recaptured in all three winter sessions and maintained its weight at 16 grams. An individual male at Grasslands in upland habitat lost weight from 24 grams in early winter to 22.25 grams when captured in mid-winter. Another at Onefour

Figure 7: Total number of *P. maniculatus* caught in the three study areas (Grasslands, Border, Onefour) during early, mid, and late winter in upland, coulee, and roadside habitats.



maintained his weight between 17 and 17.5 grams when captured in early and then again in late winter. Survival duration for these three males were 125+days, 73+ days, and 137 days (known since dead in trap on last day) respectively. In early winter, the overall proportion of animals weighing less than or equal to 15 grams was 39% compared to 61% of animals weighing more than 15 grams. In mid-winter, the proportion changed to 33% versus 67% and in late winter, 7% versus 93% (Table 7). Biomass values were highly significant for study areas ($p<0.01$), winter sessions ($p<0.01$), area x winter session ($p<0.001$), and significantly different for habitats ($p<0.05$), and area x habitat ($p<0.05$) interaction (Table 8). The relative biomass was the greatest at Grasslands and least at Onefour during early winter. But by late winter, the biomass was highest at Onefour and lowest at the Border (Figure 8). There was a decline in overall biomass of *P. maniculatus* from early to late winter at the Border and Grasslands (Figure 8). Multiple comparison of least square means (Table 9) showed highly significant differences in biomass values for the same study areas as for capture data; Border VS Grasslands ($p<0.01$), Grasslands VS Onefour study areas ($p<0.01$). For the habitats however, there were significant differences in biomass values between coulee and upland habitats ($p<0.01$), unlike those for capture data where no significant differences were observed for any particular pairs of habitats ($p>0.1$). Winter biomass values resulted in significant differences between early and late winter ($p<0.05$) and in only moderate significance between early and mid winter ($p<0.1$).

Table 7: Total number of subadult (≤ 15.0 g) and adult (> 15.0 g) *P. maniculatus* trapped during the winter in each study area and habitat type.

Study Area	Habitat	Early Winter		Mid Winter		Late Winter	
		Sub	Adult	Sub	Adult	Sub	Adult
Onefour	Upland	0	0	0	0	0	2
	Coulee	0	0	0	0	0	7
	Road	0	2	1	0	1	9
	Total	0	2	1	0	1	18
Grasslands	Upland	24	28	0	2	0	1
	Coulee	8	26	1	1	0	4
	Road	-	-	0	1	0	1
	Total	32	54	1	4	0	6
Border	Upland	10	14	0	0	0	0
	Coulee	6	4	0	0	1	2
	Road	-	-	0	0	0	0
	Total	16	18	0	0	1	2
Grand Totals		48	74	2	4	2	26

Table 8: Analysis of variance for biomass (g/plot) of *P. maniculatus* for study areas, habitats, winter period, and the interaction of these.

Dependent Variable: BIOMASS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	36	397695.17149	11047.08810	3.03	0.0010
Error	32	116545.61489	3642.05047		
Corrected Total	68	514240.78638			

R-Square	C.V.	Root MSE	BIOMASS Mean
0.773364	176.7674	60.349403	34.140580

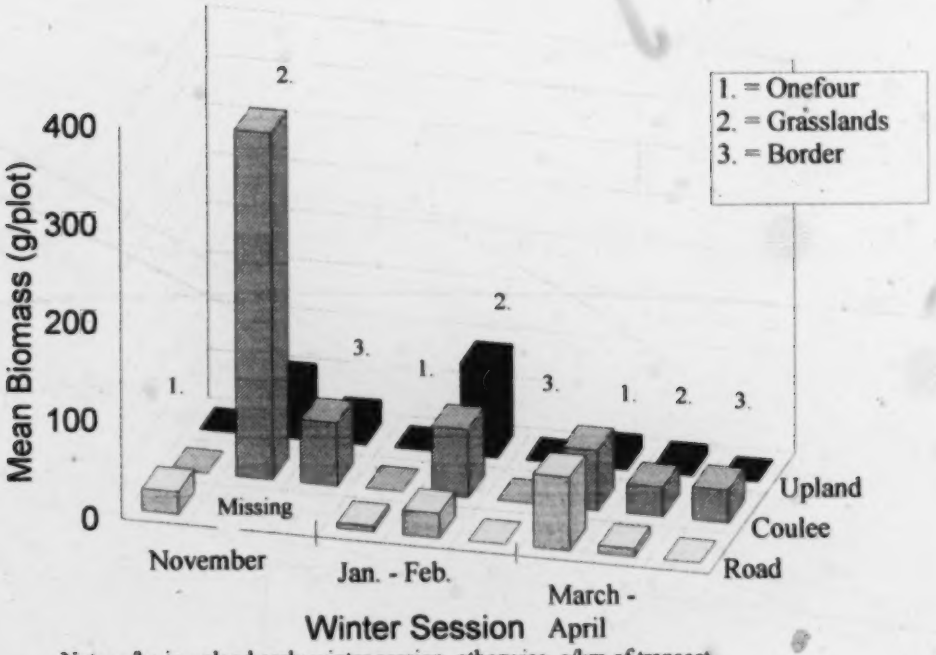
Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	59212.451053	29606.225526	8.13	0.0014
HABITAT	2	37867.219682	18933.609841	5.20	0.0111
AREA*HABITAT	4	53992.526118	13498.131530	3.71	0.0137
REP(AREA*HABITAT)	18	77275.507857	4293.083770	1.18	0.3327
WINTER	2	44936.652620	22468.326310	6.17	0.0054***
AREA*WINTER	4	95345.263259	23836.315815	6.54	0.0006***
HABITAT*WINTER	4	29065.550900	7266.387725	2.00	0.1190

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	59212.451053	29606.225526	6.90	0.0060***
HABITAT	2	37867.219682	18933.609841	4.41	0.0276**
AREA*HABITAT	4	53992.526118	13498.131530	3.14	0.0399**

* p<0.1, ** p<0.05, *** p<0.01

Figure 8: Relative mean biomass (g/plot) of *P. maniculatus* in Grasslands, Border and Onefour during early, mid, and late winter in upland, coulee and roadside habitats.



Note: g/ha in upland early winter session, otherwise, g/km of transect.

Table 9: Multiple comparison of least square means for biomass (g/plot) of *P. maniculatus* between study areas, habitats, and winter periods.

Standard Errors and Probabilities calculated using the Type III MS for REP(AREA*HABITAT) as an Error term

Dependent Variable: BIOMASS

AREA		BIOMASS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	LSMEAN Number
(Border)	BRD	16.7157407	14.6220664	0.2679	1
(Grasslands)	GRS	95.5122685	19.6855593	0.0001	2
(Onefour)	ONFR	18.8185185	11.9388672	0.1324	3

Pr > |T| H0: LSMEAN(i)=LSMEAN(j)

i/j	1	2	3
1	.	0.0030***	0.9125
2	0.0030***	.	0.0037***
3	0.9125	0.0037***	.

HABITAT		BIOMASS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	LSMEAN Number
(Coulee)	CUL	75.4759127	13.1495403	0.0001	1
(Roadside)	RD	38.7637500	20.8004284	0.0788	2
(Upland)	UPLD	16.8068651	13.1495403	0.2174	3

i/j	1	2	3
1	.	0.1504	0.0044***
2	0.1504	.	0.3808
3	0.0044***	0.3808	.

WINTER	BIOMASS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0
EAR	79.8092130	19.7982686	0.0008
LATE	25.1407407	12.3528251	0.0568
MID	30.1757407	17.9009442	0.1091

Pr > |T| H0: LSMEAN(I)=LSMEAN(j)

i/j	1	2	3
1	.	0.0308**	0.0779*
2	0.0308**	.	0.8195
3	0.0779*	0.8195	.

* p<0.1, ** p<0.05, *** p<0.01

The male:female ratio shifted from 1:1.4 (51 males, 71 females) in early winter to 1:1 (3 males, 3 females) in mid winter and 2.1:1 (19 males, 9 females) in late winter (Table 10).

The number of recaptures within trapping sessions at different trap stations was 41 in early winter and 10 in late winter. This enabled calculation of distances travelled by individuals. The greatest distances travelled by a male and a female in early winter was 250 meters. In mid-winter, recapture rates were inadequate to determine distances travelled. Distances travelled by males in late winter were considerably greater than by females and increased from early to late winter. One male individual at Onefour moved 1000 meters between two coulees while another moved 500 m from an upland to roadside habitat and still another individual moved 660 meters between trapping stations. The greatest distance moved by a female between trap stations was 120 meters during late winter.

When the number of trap stations with few and with many mice increase, it is an indication of aggregation (Metzgar and Hill 1971). Aggregation of individuals was suggested on two occasions by a male and female (not reproductively active) being caught in one trap at the same time. Both occurrences were in coulee habitats at the Border, one in early the other in late winter. Additionally, some traps resulted in the capture of more than one individual at one trap station over the four trapping days indicating range overlap. This occurred on 34 occasions in early winter, and on 8 occasions in late winter, out of a total 275 capture occasions, or 34/216 = 15.7% of the time in early winter, 0/6 = 0% in mid winter, and 8/53 = 15.1% of the time in late winter, for a total of 42/275 = 15.3% for all trap occasions. Index of dispersion values were greater than one for all

Table 10: Total number of male and female *P. maniculatus* caught over the three winter periods at Grasslands, Onefour, Border in upland, coulee, and roadside habitats.

Study Area	Habitat	Early Winter		Mid Winter		Late Winter	
		M	F	M	F	M	F
Onefour	Upland	0	0	0	0	2	0
	Coulee	0	0	0	0	6	1
	Road	2	0	0	1	6	4
	Total	2	0	0	1	14	5
Grasslands	Upland	18	34	1	1	0	1
	Coulee	13	21	1	0	2	2
	Road	-	-	1	1	1	0
	Total	31	55	3	2	3	3
Border	Upland	16	8	0	0	0	0
	Coulee	2	8	0	0	2	1
	Road	-	-	0	0	0	0
	Total	18	16	0	0	2	1
Grand Totals		51	71	3	3	19	9

* one value missing due to escape of individual.

transects except for one, indicating that population distribution was clumped over the winter (Appendix 3).

Cold temperatures (Appendix 1, 2) and deep snow during the mid winter trapping session probably contributed to low number of captures (Appendix 3). Small mammal activity, as indicated by capture rates, ceased during extremely cold (<-40°C overnight) and windy nights, and no animals were trapped; activity resumed once the temperature warmed and the winds died down. As the temperatures increased to about -15°C, small mammals were observed travelling on top of the snow surface for short lengths of time before reentering their subnivean holes and tunnels.

Throughout the winter period, no sign of actual breeding or production of litters was apparent; females were not lactating, pregnant or perforate, while only three males were semi-scrotal in mid-March at Onefour where spring-like conditions were earlier.

Vegetation Height and Litter Depth:

Differences in vegetation characteristics were apparent between study areas and habitat types (Table 11). Vegetation height (Appendix 4) differed significantly ($p<0.05$) for study areas, and was highly significant ($p<0.01$)for habitat types. Litter depth (Appendix 5) was highly significant ($p<0.01$)for both study areas and habitat types. The interaction of study area x habitat was not significant for either vegetation height or litter depth ($p>0.1$).

Multiple comparison of least square means showed that vegetation height was significantly different ($p<0.01$) between Grasslands and Onefour study areas (Appendix 6).

Table 11: Mean habitat characteristics for upland, coulee, and roadside habitats in Border, Onefour, and Grasslands study areas.

BORDER:

Habitat Characteristics (n=30)	Habitat Type			Mean
	Upland	Coulee	Roadside	
% Grass Cover	32	75	57	55
% Forb Cover	1	1	3	2
% Shrub Cover	13	15	14	14
% Cacti	2	<1	2	2
% Bare Ground	11	4	18	11
% Dung	1	2	<1	1
% Stone	2	0	<1	<1
% Club Moss	29	2	3	11
% Lichen	7	<1	2	3
Vegetation Height (cm) (n=150)	10.8	26.2	20.6	19.2
Litter Depth (cm) (n=150)	0.8	3.8	3.1	2.6

ONEFOUR:

Habitat Characteristics (n=30)	Habitat Type			Mean
	Upland	Coulee	Roadside	
% Grass Cover	47	73	83	68
% Forb Cover	2	5	2	3
% Shrub Cover	9	19	3	10
% Cacti	<1	0	0	<1
% Bare Ground	6	2	10	6
% Dung	<1	<1	<1	<1
% Stone	<1	<1	<1	<1
% Club Moss	28	<1	1	10
% Lichen	6	<1	<1	2
Vegetation Height (cm) (n=150)	14.3	25.6	26.1	22.0
Litter Depth (cm) (n=150)	2.5	5.3	4.0	3.9

GRASSLANDS:

Habitat Characteristics (n=30)	Habitat Type			Mean
	Upland	Coulee	Roadside	
% Grass Cover	58	67	71	65
% Forb Cover	2	7	3	4
% Shrub Cover	6	14	6	9
% Cacti	0	0	<1	<1
% Bare Ground	1	4	11	5
% Dung	<1	<1	<1	<1
% Stone	<1	<1	1	<1
% Club Moss	29	6	5	13
% Lichen	3	1	2	2
Vegetation Height (cm) (n=150)	11.5	20.6	16.8	16.3
Litter Depth (cm) (n=150)	2.0	3.5	2.5	2.7

Onefour had the tallest vegetation, followed by the Border and Grasslands. Highly significant differences for vegetation height were apparent between coulee and upland ($p<0.01$), and roadside and upland ($p<0.01$) habitats (Appendix 6). Vegetation was significantly taller in the linear habitats than in the uplands. Litter was significantly different between the Border and Onefour ($p<0.01$), and between Grasslands and Onefour ($p<0.01$) (Appendix 7). Onefour had the deepest litter, followed by the Border and Grasslands, which were not significantly different from each other ($p>0.1$). There was a highly significant difference in litter depth between coulee and roadside ($p<0.01$), roadside and upland ($p<0.01$), and between coulee and upland habitats ($p<0.01$) (Appendix 7). Coulee habitat had the deepest litter cover, followed by roadside, then uplands.

Ground Cover Analysis:

Percent grass cover was significantly different between study areas ($p<0.05$), habitat types ($p<0.01$) and area by habitat type interaction ($p<0.05$) (Appendix 8). Percent forb, percent shrub cover, moss and lichen were significantly different between habitat types only ($p<0.05$). Percent cacti and cattle dung were significantly different only between study areas ($p<0.05$), whereas percent bare ground was significantly different between areas ($p<0.05$) and between habitats ($p<0.01$). Percent stone cover was significantly different for area and habitat interaction only ($p<0.05$).

The multiple comparison of least square means for cover analysis are shown in Appendix 9. At Onefour, grass cover was the highest, cacti cover was low (equal to

Grasslands), while dung, stone, moss, lichen were the lowest compared to Grasslands and the Border. Percent forb, bare ground, and shrub were intermediate.

At Grasslands, percent forb and moss were the highest, percent shrub and bare ground were the lowest, while percent grass, cacti (equal to Onefour), cattle dung, stone, and lichen were intermediate compared to the other study areas.

At the Border, percent shrub, cacti, bare ground (almost twice that of Grasslands and Onefour), cattle dung, stone, and lichen were the highest, percent grass and forb were the lowest, and percent moss was intermediate compared to the other study areas.

Percent grass cover was much higher in coulee and roadside habitats than in uplands. Roadside habitats exhibited the largest % of bare ground. Coulee habitats had the greatest amount of forbs, shrubs, and cattle dung, while uplands had the greatest amount of club moss and lichen.

Based on the above ground cover composition, it appears that the range condition at Onefour was superior to the other two study areas with least cattle dung per area and less increaser species such as lichen, cacti, and moss. The poorest range condition and highest intensity of grazing pressure appeared to be at the Border, which also was the area with lowest small mammal captures in late winter and lower captures in early winter than Grasslands.

Trapping results (Table 3) indicated that deer mice were more common in upland habitat with less dense and lower vegetation cover in early winter compared to linear habitats with more dense, higher vegetation cover. In mid winter, there was no difference. In late winter, *P. maniculatus* were more common in linear habitats with higher and denser

vegetation. They did not appear to be deterred by stone cover and bare ground in roadside habitat.

Snow Depths:

Mean annual snowfall was above average (Table 1) for the winter months of 1995-1996 in all three study areas. Mean snow depths (cm) ± standard error of the mean (S.E.M.) for each study area, habitat, and winter session are shown in Table 12. Highly significant differences in mean snow depths were apparent among study areas, habitats, and winter periods ($p<0.001$), and there were interactions of area x habitat, and habitat x winter ($p<0.001$) (Table 13).

Differences in total average accumulations of snow between study areas during the period of trapping are illustrated in Figure 9. Overall, Onefour had significantly less snow than either Grasslands or the Border ($p<0.01$) (Appendix 10). The Border region consistently had the most snow followed closely by Grasslands ($p<0.05$).

There was significantly deeper snow in mid winter than during either early or late winter ($p<0.01$) (Appendix 10). Differences in snow depths, although significant ($p<0.05$), were less between late and early winter (Appendix 10). Coulee and roadside habitats had significantly greater snow than upland habitats ($p<0.01$). In early winter, when snow accumulations were minimal, deer mice were found more commonly in upland habitat (Figure 7). In mid winter, there was no difference in captures between habitats. In late winter, where snow free-zones were more prevalent in some of the linear habitats, especially along southern exposed slopes of coulees and roadside ditches, than

Table 12: Mean snow depths (cm) ± S.E.M. in the three study areas in three habitat types over three winter periods.

Area	Winter Period	Habitat	Mean Snow Depth (cm) ± S.E.M.
Border	Early	Coulee	5 ± 0.1 (n = 30)
		Roadside	-
		Upland	5 ± 0.3 (n = 60)
	Mid	Coulee	33 ± 0.1 (n = 30)
		Roadside	31 ± 0.4 (n = 30)
		Upland	27 ± 0.2 (n = 30)
	Late	Coulee	5 ± 1.8 (n = 30)
		Roadside	14 ± 1.1 (n = 30)
		Upland	12 ± 0.3 (n = 30)
Grasslands	Early	Coulee	5 ± 0.1 (n = 30)
		Roadside	-
		Upland	3 ± 0.3 (n = 60)
	Mid	Coulee	25 (n = 10)
		Roadside	41 (n = 10)
		Upland	19 (n = 10)
	Late	Coulee	9 ± 0.7 (n = 30)
		Roadside	7 ± 2.4 (n = 30)
		Upland	6 ± 0.1 (n = 30)
Onefour	Early	Coulee	0
		Roadside	0
		Upland	0
	Mid	Coulee	37 ± 0.2 (n = 30)
		Roadside	24 ± 0.2 (n = 30)
		Upland	14 ± 0.1 (n = 30)
	Late	Coulee	4 ± 2.1 (n = 30)
		Roadside	1 ± 0.1 (n = 30)
		Upland	0.3 ± 0.1 (n = 30)

Table 13: General linear models procedure for snow depths (cm) for study area, habitat, and winter, and the interaction of these main effects (same as ANOVA).

Dependent Variable: SNOW

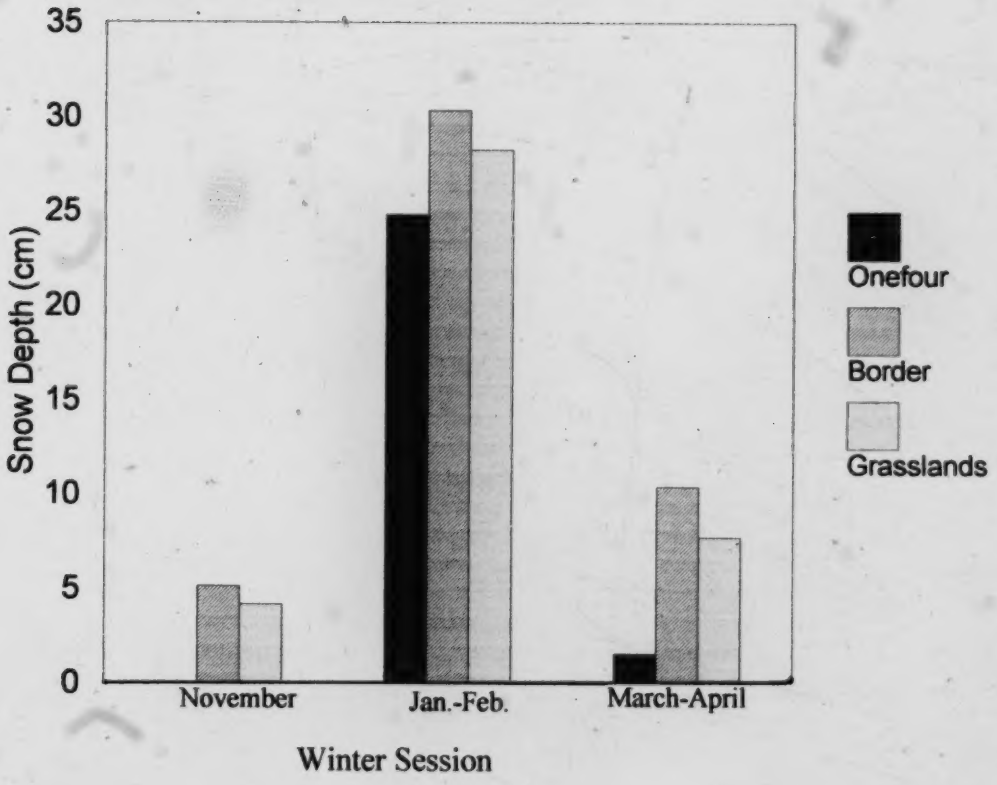
Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP(AREA*HABITAT)	18	104.35398355	5.79744353	0.54	0.9147
WINTER	2	4665.81353526	2332.90676763	217.69	0.0001***
AREA*WINTER	4	26.93500401	6.73375100	0.63	0.6458
HABITAT*WINTER	4	468.23293877	117.05823469	10.92	0.0001***

Tests of Hypotheses using the Type III MS for REP(AREA*HABITAT) as an error term

Source	DF	Type III SS	Mean Square	F Value	Pr > F
AREA	2	559.75889083	279.87944542	48.28	0.0001***
HABITAT	2	298.38038496	149.19019248	25.73	0.0001***
AREA*HABITAT	4	241.85324086	60.46331021	10.43	0.0001***

*** p<0.01

Figure 9: Mean snow depths (cm) in the three study areas, Onefour, Border and Grasslands during early (November), mid (January - February), and late winter (March - April).



in the uplands, small mammals were more abundant, where they were protected from wind and temperatures were generally warmer. Significant differences in capture rates throughout the winter ($p<0.01$) were potentially attributed to varying snow conditions. With greater accumulation of snow in all habitat types during mid winter, there was a great decline in small mammal numbers captured (Appendix 3).

DISCUSSION

Food Habits of the Swift Fox:

Swift foxes are opportunistic predators and feed on a variety of available prey over the year. For much of the summer period, the prey source is more diverse than in the winter and may include small mammals, birds, eggs, insects, amphibians, reptiles, and carrion (Hines 1980). The degree of use of these prey items reflect the most available food type within an area (Rongstad *et al.* 1989). However, in southcentral California, where the primary prey base for kit foxes was mice; shifts to other sources of food did not occur even when small mammals were scarce. Consequently, fox abundance decreased due to a decline in pup survival and an increase in coyote-induced mortality (White *et al.* 1996). The same was true for kit foxes in Utah, where foxes did not compensate for a decline in their primary prey (leporids) by consuming more alternate prey (Egoscue 1975). In Nebraska, from January to August, analysis of scat samples revealed that the primary prey consumed was *Microtus ochrogaster* (prairie vole), followed closely by cattle, *Reithrodontomys megalotis* (western harvest mouse), and *Lepus sp.* (jackrabbit) (Hines and Case 1991). Rodents comprised the largest percentage of the swift fox diet in the Oklahoma Panhandle during August, and the most common species were deer mice, harvest mice, and silky pocket mice (*Perognathus flavus*). Shrews (*Sorex sp.*) were utilized to a lesser extent (Kilgore 1969). In Texas, rabbits were found to be more important in the diet during spring, summer, and early autumn, probably varying seasonally with the availability of food (Cutter 1958). In western South Dakota during

May-September important prey items were: insects, prairie dogs (*Cynomys ludovicianus*), hispid pocket mice (*Perognathus hispidus*), northern pocket gophers (*Thomomys talpoides*), deer mice, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), northern grasshopper mice (*Onychomys leucogaster*), western harvest mice, eastern cottontails, white-tailed jackrabbits, voles, shrews and cattle remains (Uresk and Sharps 1986). Seton (1929) noted that swift foxes in Alberta preyed largely on mice and often caught prairie chickens. Scat samples collected in Alberta indicated that small mammals comprised 64.1% of the diet, followed by ungulates (23.6%), lagomorphs (5.2%) and ground squirrels (2.1%) (Reynolds *et al.* 1991, unpublished data).

In the current study, trapping results indicated that deer mice were the most abundant and common species of small mammals during the winter and thus, were likely the most available to the swift fox. However, other prey sources such as lagomorphs may also be important.

Assumptions:

Several assumptions were made based on small mammal captures. Small mammal captures were assumed to represent an index of population abundance to a reasonable degree. Trapping was assumed to account for animals residing in an area at the time of trapping even during deep snow, when small mammals were presumably active in the subnivean space under the snow, which the traps penetrated. Although deep snow and cold temperatures likely contributed to lower trapping rates and hence rendered estimates of population size in mid-winter less accurate, trapping indicated that by late winter, when

snow and temperature were no longer significant factors in trapping success, small mammals were still found to be at significantly lower levels than during early winter, indicative of declines in the populations. A decline is further supported by lack of any signs of reproduction from early to late winter. Further, as many individuals caught during early winter were young animals, the majority of them probably perished at the onset of winter or dispersed, contributing to population declines in an area. This is perhaps best exemplified by the majority of individuals being new captures and not recaptures during mid and late winter. It is unlikely that most of these individuals were residents in early winter that were not captured then, considering that mark-recapture methods are presumed to account for the majority of the population by the fourth day of trapping. Further, the influx of animals in late winter at Onefour for example, indicates that *Peromyscus* is capable of reestablishing populations fairly rapidly if weather conditions are favourable. The important factor to consider for predators however, is the productiveness of these areas throughout the winter when food sources are not as diverse and abundant.

Small Mammal Species in the Prairie Regions of Southern Alberta and Saskatchewan:

Several species of small mammals residing in the prairies were not trapped during the winter of 1995-1996. There could be several reasons for this. Some species such as the western jumping mouse (*Zapus princeps*) enter hibernation, which would render it unavailable during the winter period (Whitaker 1980). In general, *Peromyscus* populations are more stable than those of most small mammals (Bronson 1983). In the year of my

study, small mammal trapping results were indicative of low population levels of all species. In other regional studies, Pat Fargey (pers. com.) in Grasslands, Doug Forsythe (pers. com.) in the Milk River area and Hal Reynolds (pers. com.) in the Suffield area all reported deer mice being the most common species. In Kansas, Clark *et al.* (1987) found that *Peromyscus* was more common than other grassland species such as *Microtus ochrogaster*.

Low species abundance and diversity were accentuated during winter trapping when small mammal mobility was reduced, and thus, the probability of capture was reduced. Although in early winter (November) a juvenile meadow vole (*Microtus pennsylvanicus)* was seen in an upland trap site at the Border region, it was not captured. A second adult meadow vole was spotted during late winter (April) on a roadside transect at Onefour and was not captured either. It can not be assumed however, that the Longworth traps and bait used were not adequate for trapping these species as they are commonly used by researchers studying voles. Deep snow could not have been a constraint, since the two individuals were observed in early and late winter respectively, when snow was not deep enough to affect the probability of capture. Therefore, the trapping protocol was assumed adequate and other species were likely missed by chance alone because of their low abundance.

Following is a list of small mammal species that could occur in the study areas: prairie shrew (*Sorex haydeni*), dusky shrew (*Sorex monticolus*), olive-backed pocket mouse (*Perognathus fasciatus*), western harvest mouse (*Reithrodontomys megalotus*), northern grasshopper mouse (*Onychomys leucogaster*), meadow vole (*Microtus*

pennsylvanicus), sagebrush vole (*Lagurus curtatus*), long-tailed vole (*Microtus longicaudus*), and western jumping mouse (*Zapus princeps*) (Smith 1993).

Factors Influencing Small Mammal Demographics Over the Winter:

Biological Factors:

Highest small mammal population densities occur at the beginning of winter and then decline over the winter (Krebs and Wingate 1985; Linzey and Kesner 1991; Metzgar 1979; Wolff and Durr 1986). This same pattern was found in two of my three study areas. A number of intrinsic factors may contribute to this trend including: poor overwinter survival, emigration, trappability and cessation of breeding (Krebs and Wingate 1985; Sadleir 1974; Wolff and Durr 1986), while extrinsic factors such as activity level (trap exposure) and weather conditions may also influence reported population trends (Diffendorfer *et al.* 1995; Metzgar 1979). During late winter, mice have to cope with exhausted food supplies and depleted fat reserves, which contributes to a decline in numbers (Hansson 1971; Howard 1949).

Except for three individuals trapped in more than one session, survival on trapping areas was assumed to be less than 70 days, the longest interval between sessions. Literature indicates that very few *Peromyscus* in the wild live one year (Schug *et al.* 1991). In northwestern Ohio, *P. leucopus* lives an average of 70 days after weaning (Rintamaa *et al.* 1976). Survival varies seasonally, between years and geographically. Mortality of autumn-born mice is significantly higher than that for spring-born mice (Schug *et al.* 1991). The estimated per cent mortality for one year ranges from 99 per cent

for *P. maniculatus bairdi* (Howard 1949), to 63-94 per cent for *P. maniculatus gracilis* for studies conducted in Michigan (Manville 1949). *Peromyscus* numbers can decline relatively rapidly during the winter, with mortality of about 26%/month and only about 1/4 of the animals going into the winter surviving until the following breeding season (Beer and MacLeod 1966). Low winter survival has profound effects on density, which results in decreased residence times in an area and low densities that may persist all year (Krohne 1989).

During the present study, small mammal abundance was apparently low compared to other years (private landowners, pers. comm.) and averaged only 1.4 mice/ha in early winter when densities were considered highest for the winter. A capture success rate of about 10.0% or 11.1 mice/ha represent normal population densities for *Peromyscus* (Terman 1968). Trapping success for the whole winter was only 1.74% (163 captures / 9360 trap-nights). *P. maniculatus* normally fluctuate over 2.7 years (Terman 1968) and populations of *P. maniculatus* can remain low for up to 3 years, where capture success can be as low as 0.04% (Herman and Scott 1984). However, temporal variations in abundance of *Peromyscus* are considered small in comparison to other small mammals (Terman 1966). These fluctuations are influenced by environmental and biological factors (Steinhoff 1976). Yearly and seasonal variations in small mammal biomass and species composition is a regular occurrence; often populations reach similar low densities across all grassland habitats (Grant and Birney 1979). Reasons for these lows are speculative and may be due to a combination of factors such as availability of food, weather patterns, drought, and disease (Herman and Scott 1984).

In the present study, animals did not reproduce from early November to mid-April in accordance with studies conducted in Utah by Cranford (1984). In northern environments, reproductive activity of small mammals is restricted to a few months by low temperatures and short growing seasons (Millar *et al.* 1979). Timing of breeding is affected by yearly differences in temperature (Millar and Gyug 1981), initiation of snow melt (Sleeper *et al.* 1976), and the abundance of food (Sadleir 1974; Taitt 1981). The onset of breeding by *P. maniculatus* can differ by as much as 4 weeks in Alberta (Millar *et al.* 1985). In the Rocky Mountains of Alberta, earlier snow melt and thus, earlier availability of food results in earlier breeding and larger litters of *P. maniculatus* in open habitats (Millar *et al.* 1985). However, these same habitats also exhibit higher winter mortality, due to exposure to harsher environmental conditions than protected forested habitats (Sharpe and Millar 1991).

In my study, the relatively stable male to female ratio of *P. maniculatus* in early winter shifted to a higher proportion of males to females by late winter. This could be attributed to several factors. In response to a sudden rise in temperature (Sadleir 1974) animals disperse to search for mates (King 1983) and as such, the greatest number of newcomers appear associated with increased movements (Fairbairn 1977[b]). Movements by *P. maniculatus* in this study ranged from a high of 250 m in early winter, to a high of 1000 m by a male in late winter. Males appear to explore new areas more than females (Harland *et al.* 1979), and thus their home ranges increase relative to females (King 1983; Metzgar 1979; Schug *et al.* 1991). Hence, male populations of *P. maniculatus* are mainly determined by spacing behaviour and dispersal, while female population densities are

controlled by mortality resulting in declines of female densities in the spring, and an increase in the ratio of males to females (Fairbairn 1977[a]). The increased travel by males searching for mates during the onset of breeding results in increased probability of capture (Metzgar 1979; Stickel 1968; Terman 1968) and in a male capture bias (Xia and Millar 1989). Warmer temperatures and the earlier arrival of spring at Onefour probably contributed to increased captures.

Recapture rates from early to late winter were quite low and capture of new untagged animals between winter sessions was prevalent. When an animal disappears from an area it is the result of mortality or emigration (Fairbairn 1977[b]). If increased movement predominates, it is reflected by both an increased loss of animals, but counteracted by an increased rate of new recruits (Fairbairn 1977[b]). Mice will often move onto and off of study areas continually (Fairbairn 1977[b]). Spatial and temporal variation in abundance are affected by the rate and pattern of movements (Pulliam and Danielson 1992). Normally, a high percentage of animals captured in a certain area are transients and consist generally of young or young adults (Blair 1940; Blair 1951; Stickel and Warbach 1960) with a greater proportion of juvenile deer mice dispersing than adults (Wolff 1989). Animals in dense populations will move shorter average distances than individuals in less dense or sparse populations (Bendell 1959; Bendell 1961; Stickel 1960). In the Edmonton area, Kucera and Fuller (1978) did not recapture any individuals between October and March because of animals migrating. Populations of *Peromyscus leucopus* in Ontario were in a constant state of flux throughout the winter trapping period (Harland *et al.* 1979).

Small mammals were aggregated and populations were clumped throughout the winter trapping. Mice during autumn and winter are in groups (Kucera and Fuller 1978; Madison *et al.* 1984; Millar and Derrickson 1992; West 1977), while in spring and summer during the breeding season, spacing is more regular or less aggregated (Eisenberg 1968; Fairbairn 1977[b]). *Peromyscus* during the winter often nest singly or in pairs, but are sometimes found in groups as large as five mostly consisting of non-relatives, often in male-female pairs (Wolff and Durr 1986). In winter, small mammal intraspecific aggression is reduced due to non-breeding status (West 1977). Small mammals tend to be more aggregated at low population densities, while at higher densities populations are more uniform (Grant and Morris 1971). Benefits of aggregation are heat conservation (Howard 1950) and a concentrated food supply, which increases overwinter survival of animals (Wolff 1989).

In the present study, biomass values of *P. maniculatus* did not exactly follow the trend for total captures in each area during mid and late winter. An increase in biomass values compared to total captures was due to an overall increase in average weights of animals caught during mid-winter, but a decrease in numbers caught. A greater proportion of animals weighed more than 15.0 grams, the trend being reversed from early winter captures when there were still many immature animals. Weights of individuals recaptured over the winter remained fairly stable, although the sample size was small. This was in contradiction to Stebbins' (1977) study where there was a marked decline in weights of *P. maniculatus* over the winter.

The Effects of Vegetation and Ground Cover:

Over the last few decades, increased grazing pressure by livestock has resulted in habitat deterioration of the remaining natural prairie grasslands (Coupland 1987). This has had an impact on the diversity and abundance of the native flora and fauna. The use of particular areas and habitats within the range of a species depends on the distribution of available resources, climatic conditions, and the presence of other species (Krebs 1972). Shifts in habitat use may be influenced by changes in the availability of protective cover (Barnum *et al.* 1992).

Decreased vegetation height and litter depth, a marked decrease in grasses, increased bare ground and dung, and greater levels of increaser or invader species such as sage brush, cacti, and club moss are considered to indicate higher grazing intensity and poorer range condition (Smoliak *et al.* 1988) and will result in lower densities of small mammals (Baker 1968). Based on the above criteria, the Onefour study area exhibited healthier range conditions than the other two study areas. Often times, these differences in vegetation characteristics can influence small mammal abundance, distribution, survival and species' composition (Birney *et al.* 1976; LoBue and Darnell 1959; Rosenzweig 1973).

P. maniculatus were commonly caught in upland habitat during early winter where vegetation was shorter and sparser and forbs were abundant (including club moss). Researchers in Kansas (McMillan and Kaufman 1995), Minnesota, and Maryland (Barnum *et al.* 1992) found that *Peromyscus* used habitats abundant in forbs and bare ground where the increased risk of predation was probably outweighed by the increased availability of

food in these areas (Kaufman *et al.* 1988). In low cover sites, plants deposit a much higher proportion of their energy into seeds than plants at high cover sites, which ultimately favours the granivorous deer mouse (Grant and Birney 1979). Fall food supply depends on weather during the previous spring seeding (Wolff 1989). Rainfall pattern influences the availability of food for small mammals such as vegetation, seed, and insect production (Whitford 1976). An increased food supply can result in increased overwinter survival and earlier initiation of breeding (Bendell 1959; Flowerdew 1973). In British Columbia, the addition of food to study sites resulted in increased density, higher immigration, smaller home ranges, higher reproductive rates, and higher body weights for *P. maniculatus* (Taitt 1981).

In late winter, small mammals were more commonly trapped in linear habitats (coulees and roadsides) where vegetation was taller and denser, and plant litter was deeper. Roadside habitats with a predominance of bare ground were not selected against and *P. maniculatus* were often captured near rock cover, when present, especially along roadsides. In Kansas on recently burned areas, *P. maniculatus* selected areas with a high proportion of exposed soil, limestone and dense grass cover (Kaufman *et al.* 1988). Limestone breaks provide ideal habitat for nests and protection from predation (Kaufman *et al.* 1988). Density and depth of plant litter can be influenced by such factors as plant productivity, fire intensity, and grazing; areas with greater cover reduce the risks of predation (Clark and Kaufman 1991), provide shelter from inclement weather and a favourable microclimate (Grant and Birney 1979).

P. maniculatus is the most wide spread in North America, it is highly adaptive, and considered a habitat generalist (Whitaker *et. al* 1980). Although trapping results indicated a significant difference in numbers of *P. maniculatus* between habitats during early and late winter, the results were not highly significant and trapping results did not indicate consistency in animals being more abundant in one habitat type over another throughout the winter. Thus, the abundance and distribution of *P. maniculatus* were governed by a combination factors not only attributed to vegetation characteristics.

The Effects of Snow and Temperature:

In the prairie grasslands, snow cover can vary widely from year to year geographically and within winter period. Wind redistributes snow throughout the winter, removes it from the uplands and deposits it in roadside ditches and coulees where taller vegetation and depressions keep the snow in place. Therefore, linear habitats have deeper and softer snow than the uplands. Hardness and density of snow are governed by exposure to wind, topography, vegetation characteristics, and winter freeze-thaw cycles. Uplands are more exposed to the wind, have flatter topography and lower vegetation, and thus, snow in these habitats is more crusted and shallower than in linear habitats. The duration of snow cover, thickness, hardness and density influence small mammal population size, mortality, and movement (Merritt 1984).

Lowest capture rates of small mammals occurred in mid-winter when temperatures were the coldest and high winds prevailed. It was not uncommon for overnight temperatures to drop to -40°C. Researchers have found that activity of mice was reduced

during periods of very cold temperatures (Thomsen 1945), low food availability (Tannenbaum and Pivorun 1984), and high winds (Marten 1973), and was influenced by light and moisture (Falls 1968). Linduska (1950) found that small mammal captures declined after November and none were captured from January to February. Small mammal numbers in Alberta showed a sharp decline in late January-early February even when warmer temperatures prevailed (Kucera and Fuller 1978). Declines result from cessation of reproduction, a decline in food supply and accessibility to food, decline in fat reserves, or restricted travel caused by cold temperatures and snow conditions (Baker 1968). During this time, some individuals enter torpor for at least part of the winter (Stebbins 1971), sometimes for short periods of time commencing at daybreak and terminating by the afternoon (Hill 1983). They also spend more time in their nests, decrease activity, and decrease foraging while relying more on stored food supplies (Grodzinski and Wunder 1975). Ultimately, this helps to conserve energy needed for thermogenesis (Stebbins 1984). The highest frequency of torpor by *Peromyscus* occurs during the coldest months of the year, December-February, when nearly 40% of the animals enter this state (Pierce and Vogt 1993). In the current study, capture rates increased slightly once the cold and wind subsided.

During late winter, large puddles were present in uplands and rivers formed in coulees and roadside ditches. Snow free zones first appeared on the southern exposed slopes of coulees and roadside ridges, which provided mice with a warm dry habitat, access to food, and protection from predators (Clark and Kaufman 1991). During fluctuating water levels shifts in home ranges occur (Pearson 1953). During post-snow

melt, deer mice were found to travel greater distances. One individual travelled 1000 m during snow melt in late winter. Steinhoff (1976) recorded individuals travelling 800-900 meters. Seasonal migrations by *P. boylei* in California during spring, showed movements into areas of snow melt and home ranges varying between 0.1-10 acres, dependent on habitat, food supply, weather, age, sex, population density, and activity (Storer *et al.*1944).

Implications for Swift Fox Survival Over Winter:

Small mammals are an important part of the swift fox diet, especially during the winter when other prey sources are limited (White *et al.* 1996; Hines and Case 1991). To what extent starvation plays a role in swift fox mortality in the northern limits of its range has not been investigated. At least four foxes necropsied in the winter of 1995-1996 died of starvation (Jasper Michie, pers. comm.). Potentially more died of the same cause; teeth analysis of dead foxes in 1996, revealed that many exhibited nutritional deficiencies, gum disease, and poor overall teeth condition (pers. obs.). Starvation among arctic foxes (*Alopex lagopus*) for example, is a major cause of mortality during winter, especially among young foxes when food abundance is limited (Prestrud 1991). It is not uncommon for foxes to remain without food for 10-14 days at a time during the winter months. This implicates a highly variable food supply available to the fox due to either the individual's capacity of finding food being variable or because the food is highly dispersed spatially or both (Prestrud 1991). Depleted fat reserves in Arctic foxes can also add to food stress by late winter (Prestrud 1991).

Feeding and the search for food are predominant activities of the majority of wild animals (Rozin 1976). Activity patterns and daily energy expenditures reflect the costs and efficiencies of obtaining food (Robbins 1983). An animal will strive to minimize time and energy expenditures for obtaining food and maximize food intake. As food availability decreases, foraging effort must increase. The animal is thus forced to expend more time and energy in acquiring the necessary food. If food availability becomes extremely low and energy requirements cannot be met, animals will then emigrate to more productive areas or reduce hunting effort to conserve energy reserves (Robbins 1983). Swift fox in Canada can occupy home ranges of up to 32 km^2, 2.5 times that of the closely related kit fox in the more southern portions of the range in Mexico (Axel Moehrenschlager, unpublished data). As winter progresses, swift fox home range and mortality increase from January to April, when the peak is reached (Axel Moehrenschlager and Jasper Michie, pers. comm.), and then slowly declines after April when other food becomes available. As distances travelled increase, the potential for exposure to higher predation risks by coyotes (*Canis latrans*) and birds of prey also increase.

In the northern part of the swift fox range there is a lower density and diversity of alternative prey (Simpson 1964) and prey populations are variable from year to year. In the kit fox range of Arizona, nocturnal rodents are the most available throughout the year (Zoellick and Smith 1992), whereas lagomorphs (black-tailed jackrabbits and desert cottontails) are not abundant (Zoellick and Smith 1992). In areas with low biomass of small mammals, kit foxes adjust their home ranges according to the available prey biomass

(White *et al.* 1996) and tend to have larger exclusive home ranges (Zoellick and Smith 1992).

The average daily amount of food consumed by a captive swift fox is 227 g (Egoscue 1962), but may vary based on the availability of water ranging from 7-11 ounces/day (198-312 g/day) in captive conditions (Clio Smeeton, pers. com.). Amounts are probably substantially lower in the winter. The present study suggests that lack of food likely contributes to a high percentage of swift fox mortality over the winter. Biomass values for small mammals were already low at the onset of winter and declined significantly from early to late winter. Additionally, deep and crusted snow probably limited prey access by the fox, especially during mid-winter. For *P. maniculatus*, abundance and distribution were dependent on a combination of biological and environmental factors, which probably influenced where swift foxes focused their hunting activities. Findings of this study support release of foxes in the fall rather than spring, when small mammal prey are more abundant, improving the chances for swift fox survival.

Potential Plans of Action for Increasing Reintroduction Success, a Pro-active Approach:

As the need for long term biological studies increase to help improve the understanding of ecosystem functions and relations, while allocation of funds to long term projects decrease, it is necessary to come up with creative approaches to predicting long term effects in a short length of time. One approach to this, is the use of predictive

models, however, these models often prove to be too artificial to deal with the realities of a highly variable natural environment.

Therefore, I suggest two immediate plans of action that may improve the potential survival rate of wild swift foxes upon release into the Canadian prairies. The first, is to assess winter prey abundance including small mammals, lagomorphs, and upland birds prior to swift fox release. The second, is management of current coyote populations, which are major contributors to swift fox mortality (Axel Moehrenschlager, unpublished data), in swift fox release sites. Small mammals are a major food source for swift fox during the winter, and their abundance fluctuates or cycles over several years, however, the interval and duration of these cycles is not known, but appear to occur on a regional not local level. During periods of low prey abundance, releases should be discouraged. When prey is abundant, releases should be maximized. As short term monitoring studies are carried out each year, the potential for predicting long term population cycles will increase along with elucidating potential reasons for these fluctuations, i.e.; weather trends.

Recommendations for Future Studies:

Winter small mammal population dynamics and movement patterns affect swift fox hunting behaviour and the success of obtaining sufficient amounts of food, and as such, future studies should try to relate these factors focusing on such aspects as swift fox feeding strategies under various snow conditions and food habits by extensive scat analysis (in progress). Swift fox hunting behaviour in relation to snow ecology is important in

determining constraints imposed on hunting success under varying winter conditions. Red foxes (*Vulpes vulpes*) for example, detect prey under the snow with their keen sense of smell and hearing (Formozov 1964) and then pounce on their unsuspecting victims. They are able to find the winter nests of voles under 30 to 40 cm of snow. Foxes have been observed to make as many as 20 to 25 diggings on their daily hunting routes (Formozov 1964). As the snow becomes deeper and more dense, prey become less available. A thin layer of snow with a hard crust can be more obstructive for hunting than relatively deep and soft snow. In eastern Maine, red foxes prefer open areas for hunting, especially those areas with grass and sedge vegetation when snow is shallower. As snow depth increases, habitats with dense under storey vegetation are used. As snow depth and crusting of snow increases even further, the availability of small mammals in all habitats are restricted and the occurrence of hare in the diet increases (Halpin and Bissonette 1988; Pruitt 1978). Foxes avoid deep soft snow for travel and favour roads and trails and the wind-blown snow surfaces of open regions (Cutter 1958; Halpin and Bissonette 1988). Snow depths and structure reflect availability of predominant prey species and habitat use patterns by the fox. Until further investigations into the food habits of the swift fox are complete, the importance of prey types and the ability of the fox to switch to alternate prey sources during periods of low availability of preferred prey will be speculative.

To improve the quality of future small mammal studies in the winter more replicates are desirable so that information on the variability of the estimate can be obtained (Hayne 1978). Practically, this suggestion is sometimes difficult to meet if the trapping grids are large and manpower limited. To help off-set this difficulty, upland

regions should be trapped in a 12 x 12 grid at about 15 m intervals, which seems to be a good compromise for most studies of small mammals (Hayne 1978). Linear habitats should be trapped along transects but with only 15 m intervals between traps and a distance covering at least 1 km, possibly with assessment lines. In the winter, as travel and efficiency of trapping is impeded by cold and snow, I suggest at least 3 to 4 people working in an area at a time so that larger areas with more traps can be trapped to obtain a better estimate of small mammal populations. Trapping should be done for a week in each area to help account for small mammal inactivity during periods of extreme weather conditions. To achieve these goals, reliable and modern equipment such as snowmobiles, sleds, and amphibious all terrain vehicles would be needed to access trap sites. Heavy duty winter weather gear should also be provided. A form of communication between individuals would be an asset to ensure an extra measure of safety. Funding permitting, future work should focus on clarifying yearly differences in small mammal population dynamics by fitting the animals with radio collars to monitor survival and activity patterns more accurately throughout the winter. This should then be related to swift fox diet and hunting activities. Body condition of dead swift fox should be examined in detail to determine cause of death i.e.; lack of food.

In years of minimal snow cover it is expected that distribution of small mammals may vary where linear habitats with higher vegetation cover would probably be favoured because they provide better insulation from weather and less packing of snow in the higher vegetation zones making the subnivean space more hospitable. Access to prey by foxes under these conditions should be monitored. Crusting of snow would be more prevalent in

the wind exposed upland regions, which would probably deter foxes from hunting there. In years of high small mammal populations, swift foxes may be more reliant on them for food during the winter as their accessibility and availability are greater. During periods of small mammal lows, swift foxes would probably be under a considerable amount of food stress, resulting in their decreased survivorship, an increased vulnerability to coyote predation, and a decline in pup production. Documentation of annual differences in these responses and relationships would contribute to the management of swift foxes to help ensure their future survival.

This study is hoped to provide guidelines, spark interest, and encourage future studies on small mammal winter ecology in the prairies.

SUMMARY

1. Small mammal density and species' diversity was low in the Canadian prairies during the winter of 1995-1996.

2. Small mammal abundance was highest in the fall and then declined over the winter, except in one area where spring-like conditions were earlier and range conditions were superior. Capture probabilities indicative of population fluctuations were governed by the cessation of breeding, natural mortality, migration, activity patterns, aggregated populations, vegetation characteristics, snow conditions, and weather.

3. In early winter, when snow was not yet a contributing factor, *P. maniculatus* were concentrated in upland habitat where grasses were shorter and less dense.

4. Lowest capture of small mammals occurred in mid-winter.

5. In late winter, deer mice were more common in linear habitats with higher and denser vegetation, where there was less snow and temperatures were warmer.

6. Management decisions should focus on aspects of winter food availability and abundance, and the presence of predators when considering swift fox reintroductions.

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APPENDICES

Appendix 1: GPS co-ordinates for each transect replicate by habitat type and study area.

ONEFOUR:

UPLAND: 1. 38055E 44575N (transect runs NE from trail)
2. 3634E 4050N (transect runs N of co-ordinate)
3. 36806E 41080N (transect runs S from co-ordinate for 600m then bends E for 300m)

COULEE: 1. 37846E 44454N (transect runs N for 600m from road and S 300m from road)
2. 3615E 4185N(transect runs NW of co-ordinate)
3. 36500E 41718N (transect runs SE of co-ordinate)

ROADSIDE: 1. 38611E 42598N (transect runs S of co-ordinate)
2. 3665E 4035N (transect runs NW of co-ordinate)
3. 3690E 4034N (transect runs E of co-ordinate)

BORDER:

UPLAND: 1. 81935E 37190N (transect runs E of co-ordinate)
2. 81954E 32872N (transect runs E of co-ordinate)
3. 83385E 29169N (transect runs W of co-ordinate)

COULEE: 1. 81875E 37549N (transect runs E of co-ordinate)
2. 81819E 32802N (transect runs E of co-ordinate)
3. 83278E 28891N (transect runs W of co-ordinate)

ROADSIDE: 1. 83371E 37670N (transect runs W of co-ordinate)
2. 81874E 32843N (transect runs S of co-ordinate)
3. 82795E 28962N (transect runs W of co-ordinate)

GRASSLANDS:

UPLAND: 1. 13362E 56520N (transect runs W of co-ordinate)
2. 26807E 50602N (transect runs N of co-ordinate)

3. 24017E 56091N (transect runs S of co-ordinate for 600m then E for 300m)

COULEE: 1. 13718E 56455N (transect runs S of co-ordinate)
2. 26905E 50375N (transect runs SW of co-ordinate)
3. 23891E 56435N (transect runs NE of co-ordinate)

ROADSIDE: 1. 13658E 55709N (transect runs S of co-ordinate)
2. 27488E 50010N (transect runs E of co-ordinate)
3. 23975E 56126N (transect runs S of co-ordinate)

Note: Directions are guidelines only, and some veering will be necessary to follow transect locations exactly, this will become apparent once habitat is traversed.

Appendix 2: Table showing mean monthly temperatures (°C), minimum and maximum temperatures and monthly snowfall (cm) for Grasslands and Onefour, where information was available. First November, 1995 - 17 March, 1996 for Onefour; 1 November, 1995 - 1 April, 1996 for Grasslands.

Measurement	Station	Nov.	Dec.	Jan.	Feb.	March	Apr. 1
Extreme minimum temperature (°C)	Grasslands	-26	---	-40	-42	-35	-7
	Onefour	-22	-32	-32	-37	-28	---
Daily maximum temperature (°C)	Grasslands	16	---	5	6	9	-1
	Onefour	14	6	9	10	13	---
Monthly mean temperature (°C)	Grasslands	-5	---	-20	-10	-8	---
	Onefour	-4	-12	-21	-17	-6	---
Monthly snowfall (cm)	Onefour	23	33	---	---	---	---

Appendix 3: Table showing study areas, replicates of habitats trapped, winter trapping sessions, total small mammal captures, snow depth measurements (cm), vegetation height measurements (cm), litter depth measurements (cm), estimation of population size by the program "Capture", square root and log transformations for capture estimates, index of dispersion calculations.

OBS	REP	AREA	HABITAT	WINTER	SMAM	SNOW	VEGHT	LITTER	CAPTURE	CAP_SR	CAP_LOG	INDEX
1	1	ONFR	UPLD	EAR	0	0.00	12.26	2.33	0	0.00000	0.00000	0
2	2	ONFR	UPLD	EAR	0	0.00	14.10	3.20	0	0.00000	0.00000	0
3	3	ONFR	UPLD	EAR	0	0.00	11.10	2.50	0	0.00000	0.00000	0
4	1	ONFR	CUL	EAR	0	0.00	31.00	5.60	0	0.00000	0.00000	0
5	2	ONFR	CUL	EAR	0	0.00	21.00	4.94	0	0.00000	0.00000	0
6	3	ONFR	CUL	EAR	0	0.00	24.78	5.46	0	0.00000	0.00000	0
7	1	ONFR	RD	EAR	0	0.00	27.42	3.92	0	0.00000	0.00000	0
8	2	ONFR	RD	EAR	2	0.00	29.10	3.94	3	1.73205	0.60206	90
9	3	ONFR	RD	EAR	0	0.00	21.86	4.06	0	0.00000	0.00000	0
10	1	GRS	UPLD	EAR	18	3.73	14.34	2.78	19	4.35890	1.30103	19.98
11	2	GRS	UPLD	EAR	13	3.75	11.56	1.76	14	3.74166	1.17609	10.19
12	3	GRS	UPLD	EAR	22	3.00	8.74	1.51	23	4.79583	1.38021	30.17
13	1	GRS	CUL	EAR	2	4.61	19.64	3.40	4	2.00000	0.69897	0.16
14	2	GRS	CUL	EAR	20	4.80	19.60	3.06	31	5.56776	1.50515	30.48
15	3	GRS	CUL	EAR	12	5.00	22.68	4.00	15	3.87298	1.20412	12.51
16	1	GRS	RD	EAR	.	.	19.12	3.10	.	.	.	.
17	2	GRS	RD	EAR	.	.	14.94	2.24	.	.	.	.
18	3	GRS	RD	EAR	.	.	16.50	2.14	.	.	.	.
19	1	BRD	UPLD	EAR	5	5.30	10.94	0.80	5	2.23607	0.77815	6.52
20	2	BRD	UPLD	EAR	18	5.80	10.52	0.78	20	4.47214	1.32222	99.78
21	3	BRD	UPLD	EAR	1	4.80	11.00	0.82	1	1.00000	0.30103	0
22	1	BRD	CUL	EAR	4	5.00	27.20	3.10	4	2.00000	0.69897	12.00
23	2	BRD	CUL	EAR	2	5.30	31.28	5.32	3	1.73205	0.60206	2.00
24	3	BRD	CUL	EAR	4	5.10	20.10	3.10	4	2.00000	0.69897	12.00
25	1	BRD	RD	EAR	.	.	20.30	2.44	.	.	.	.
26	2	BRD	RD	EAR	.	.	23.22	2.72	.	.	.	.
27	3	BRD	RD	EAR	.	.	18.38	4.12	.	.	.	.
28	1	ONFR	UPLD	MID	0	13.90	12.26	2.33	0	0.00000	0.00000	0

29	2	ONFR	UPLD	MID	0	14.10	14.10	3.20	0	0.00000	0.00000	0
30	3	ONFR	UPLD	MID	0	14.00	11.10	2.50	0	0.00000	0.00000	0
31	1	ONFR	CUL	MID	0	36.95	31.00	5.60	0	0.00000	0.00000	0
32	2	ONFR	CUL	MID	0	36.30	21.00	4.94	0	0.00000	0.00000	0
33	3	ONFR	CUL	MID	0	36.65	24.78	5.46	0	0.00000	0.00000	0
34	1	ONFR	RD	MID	0	23.53	27.42	3.92	0	0.00000	0.00000	0
35	2	ONFR	RD	MID	1	24.00	29.10	3.94	1	1.00000	0.30103	0
36	3	ONFR	RD	MID	0	23.25	21.86	4.06	0	0.00000	0.00000	0
37	1	GRS	UPLD	MID	2	18.74	14.34	2.78	4	2.00000	0.69897	30.00
38	2	GRS	UPLD	MID	.	.	11.56	1.76	.	.	.	.
39	3	GRS	UPLD	MID	.	.	8.74	1.51	.	.	.	.
40	1	GRS	CUL	MID	2	25.33	19.64	3.40	4	2.00000	0.69897	30.00
41	2	GRS	CUL	MID	.	.	19.60	3.06	.	.	.	.
42	3	GRS	CUL	MID	.	.	22.68	4.00	.	.	.	.
43	1	GRS	RD	MID	1	40.64	19.12	3.10	1	1.00000	0.30103	0
44	2	GRS	RD	MID	.	.	14.94	2.24	.	.	.	.
45	3	GRS	RD	MID	.	.	16.50	2.14	.	.	.	.
46	1	BRD	UPLD	MID	0	26.81	10.94	0.80	0	0.00000	0.00000	0
47	2	BRD	UPLD	MID	0	26.78	10.52	0.78	0	0.00000	0.00000	0
48	3	BRD	UPLD	MID	0	27.44	11.00	0.82	0	0.00000	0.00000	0
49	1	BRD	CUL	MID	0	33.44	27.20	3.10	0	0.00000	0.00000	0
50	2	BRD	CUL	MID	0	33.50	31.28	5.32	0	0.00000	0.00000	0
51	3	BRD	CUL	MID	0	33.54	20.10	3.10	0	0.00000	0.00000	0
52	1	BRD	RD	MID	0	30.52	20.30	2.44	0	0.00000	0.00000	0
53	2	BRD	RD	MID	0	31.32	23.22	2.72	0	0.00000	0.00000	0
54	3	BRD	RD	MID	0	30.10	18.38	4.12	0	0.00000	0.00000	0
55	1	ONFR	UPLD	LATE	0	0.26	12.26	2.33	0	0.00000	0.00000	0
56	2	ONFR	UPLD	LATE	2	0.08	14.10	3.20	2	1.41421	0.47712	90.00
57	3	ONFR	UPLD	LATE	0	0.51	11.10	2.50	0	0.00000	0.00000	0
58	1	ONFR	CUL	LATE	0	7.88	31.00	5.60	0	0.00000	0.00000	0
59	2	ONFR	CUL	LATE	3	2.97	21.00	4.94	3	1.73205	0.60206	12.86
60	3	ONFR	CUL	LATE	4	0.60	24.78	5.46	6	2.44949	0.84510	25.71
61	1	ONFR	RD	LATE	3	0.96	27.42	3.92	4	2.00000	0.69897	6.00
62	2	ONFR	RD	LATE	2	0.60	29.10	3.94	2	1.41421	0.47712	2.00
63	3	ONFR	RD	LATE	5	0.53	21.86	4.06	5	2.23607	0.77815	20.00
64	1	GRS	UPLD	LATE	1	6.22	14.34	2.78	1	1.00000	0.30103	0
65	2	GRS	UPLD	LATE	0	6.47	11.56	1.76	0	0.00000	0.00000	0

66	3	GRS	UPLD	LATE	0	6.61	8.74	1.51	0	0.00000	0.00000	0
67	1	GRS	CUL	LATE	4	8.08	19.64	3.40	4	2.00000	0.69897	90.00
68	2	GRS	CUL	LATE	0	10.07	19.60	3.06	0	0.00000	0.00000	0
69	3	GRS	CUL	LATE	0	10.43	22.68	4.00	0	0.00000	0.00000	0
70	1	GRS	RD	LATE	1	5.69	19.12	3.10	1	1.00000	0.30103	0
71	2	GRS	RD	LATE	0	4.27	14.94	2.24	0	0.00000	0.00000	0
72	3	GRS	RD	LATE	0	11.99	16.50	2.14	0	0.00000	0.00000	0
73	1	BRD	UPLD	LATE	0	11.79	10.94	0.80	0	0.00000	0.00000	0
74	2	BRD	UPLD	LATE	0	12.46	10.52	0.78	0	0.00000	0.00000	0
75	3	BRD	UPLD	LATE	0	12.78	11.00	0.82	0	0.00000	0.00000	0
76	1	BRD	CUL	LATE	2	1.46	27.20	3.10	4	2.00000	0.69897	90.00
77	2	BRD	CUL	LATE	0	5.82	31.28	5.32	0	0	0.00000	0
78	3	BRD	CUL	LATE	1	7.67	20.10	3.10	1	1	0.30103	0
79	1	BRD	RD	LATE	0	15.15	20.30	2.44	0	0	0.00000	0
80	2	BRD	RD	LATE	0	14.89	23.22	2.72	0	0	0.00000	0
81	3	BRD	RD	LATE	0	11.86	18.38	4.12	0	0	0.00000	0

Abundance of Mice

Analysis of Variance Procedure
Class Level Information

Class	Levels	Values
AREA	3	BRD GRS ONFR
HABITAT	3	CUL RD UPLD
REP	3	1 2 3
WINTER	3	EAR LATE MID

Number of observations in data set = 81

Appendix 4: Analysis of variance for vegetation height (cm) for area, habitat, and area by habitat interaction.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	347.13608889	173.56804444	5.45	0.0141**
HABITAT	2	2316.56782222	1158.28391111	36.35	0.0001***
AREA*HABITAT	4	224.01671111	56.00417778	1.76	0.1814

* p<0.1, ** p<0.05, *** p<0.01

Appendix 5: ANOVA of litter depth (cm) for area, habitat, and the interaction of these.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	34.02535556	17.01267778	13.61	0.0003***
HABITAT	2	77.50888889	38.75444444	31.00	0.0001***
AREA*HABITAT	4	9.55751111	2.38937778	1.91	0.1523

* p<0.1, ** p<0.05, *** p<0.01

Appendix 6: Multiple comparison of least square means for vegetation height (cm) between study areas and habitats.

General Linear Models Procedure
Least Squares Means

Standard Errors and Probabilities calculated using the Type III MS for REP(AREA*HABITAT) as an Error term

AREA	VEGHT LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	19.2155556	1.8815216	0.0001	1	.	0.0782*	0.1717
GRS	16.3466667	1.8815216	0.0001	2	0.0782*	.	0.0041***
ONFR	21.4022222	1.8815216	0.0001	3	0.1717	0.0041***	.

HABITAT	VEGHT LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	24.1422222	1.8815216	0.0001	1	.	0.0719*	0.0001***
RD	21.2044444	1.8815216	0.0001	2	0.0719*	.	0.0001***
UPLD	11.6177778	1.8815216	0.0001	3	0.0001***	0.0001***	.

* p<0.1, ** p<0.05, *** p<0.01

Study Areas:

BRD=Border
GRS=Grasslands
ONFR=Onefour

Habitats:

CUL=Coulee
RD=Roadside
UPLD=Upland

Appendix 7: Multiple comparison of least square means for litter depth (cm) between study areas and habitats.

General Linear Models Procedure
Least Squares Means

Standard Errors and Probabilities calculated using the Type III MS for REP(AREA*HABITAT) as an Error term

AREA	LITTER LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	2.57777778	0.21517530	0.0001	1	.	0.7763	0.0002***
GRS	2.66555556	0.21517530	0.0001	2	0.7763	.	0.0004***
ONFR	3.99444444	0.21517530	0.0001	3	0.0002***	0.0004***	.

HABITAT	LITTER LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	4.22000000	0.21517530	0.0001	1	.	0.0032***	0.0001***
RD	3.18666667	0.21517530	0.0001	2	0.0032***	.	0.0003***
UPLD	1.83111111	0.21517530	0.0001	3	0.0001***	0.0003***	.

* p<0.1, ** p<0.05, *** p<0.01

Study Areas:

BRD=Border
GRS=Grasslands
ONFR=Onefour

Habitats:

CUL=Coulee
RD=Roadside
UPLD=Upland

Appendix 8: ANOVA for ground cover between study areas and habitats.

Dependent Variable: GRASS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	7529.40740741	289.59259259	.	.
Error	0	.	.		
Corrected Total	26	7529.40740741			

R-Square	C.V.	Root MSE	GRASS Mean
1.000000	0	0	62.85185185

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	936.96296296	468.48148148	.	.
HABITAT	2	3691.62962963	1845.81481481	.	.
AREA*HABITAT	4	1176.14814815	294.03703704	.	.
REP(AREA*HABITAT)	18	1724.66666667	95.81481481	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	936.96296296	468.48148148	4.89	0.0201**
HABITAT	2	3691.62962963	1845.81481481	19.26	0.0001***
AREA*HABITAT	4	1176.14814815	294.03703704	3.07	0.0432**

Dependent Variable: FORB

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	153.46962963	5.90267806	.	.
Error	0	.	.		
Corrected Total	26	153.46962963			

R-Square	C.V.	Root MSE	FORB Mean
1.000000	0	0	2.79629630

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	7.89851852	8.94925926	.	.
HABITAT	2	31.16740741	15.58370370	.	.
AREA*HABITAT	4	37.74370370	9.43592593	.	.
REP(AREA*HABITAT)	18	66.66000000	3.70333333	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	17.89851852	8.94925926	2.42	0.1176
HABITAT	2	31.16740741	15.58370370	4.21	0.0317**
AREA*HABITAT	4	37.74370370	9.43592593	2.55	0.0750*

Dependent Variable: SHRUB

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	1116.00000000	42.92307692	.	.
Error	0	.	.		
Corrected Total	26	1116.00000000			

R-Square	C.V.	Root MSE	SHRUB Mean
1.000000	0	0	10.66666667

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	153.55555556	76.77777778	.	.
HABITAT	2	372.66666667	186.33333333	.	.
AREA*HABITAT	4	198.44444444	49.61111111	.	.
REP(AREA*HABITAT)	18	391.33333333	21.74074074	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	153.55555556	76.77777778	3.53	0.0508*
HABITAT	2	372.66666667	186.33333333	8.57	0.0024***
AREA*HABITAT	4	198.44444444	49.61111111	2.28	0.1004

Dependent Variable: CACTI

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	30.51851852	1.17378917	.	.
Error	0	.	.		
Corrected Total	26	30.51851852			

R-Square	C.V.	Root MSE	CACTI Mean
1.000000	0	0	0.59259259

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	7.40740741	3.70370370	.	.
HABITAT	2	3.18518519	1.59259259	.	.
AREA*HABITAT	4	3.25925926	0.81481481	.	.
REP(AREA*HABITAT)	18	16.66666667	0.92592593	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	7.40740741	3.70370370	4.00	0.0365**
HABITAT	2	3.18518519	1.59259259	1.72	0.2072
AREA*HABITAT	4	3.25925926	0.81481481	0.88	0.4954

Dependent Variable: GRND

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	985.38000000	37.89923077	.	.
Error	0	.	.		
Corrected Total	26	985.38000000			

R-Square	C.V.	Root MSE	GRND Mean
1.000000	0	0	7.50000000

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	176.04222222	88.02111111	.	.
HABITAT	2	432.64222222	216.32111111	.	.
AREA*HABITAT	4	80.47555556	20.11888889	.	.
REP(AREA*HABITAT)	18	296.22000000	16.45666667	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	176.04222222	88.02111111	5.35	0.0150**
HABITAT	2	432.64222222	216.32111111	13.14	0.0003***
AREA*HABITAT	4	80.47555556	20.11888889	1.22	0.3360

Dependent Variable: DUNG

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F

Model	26	19.91407407	0.76592593	.	.
Error	0	.	.		
Corrected Total	26	19.91407407			

R-Square	C.V.	Root MSE	DUNG Mean
1.000000	0	0	0.88518519

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	5.75629630	2.87814815	.	.
HABITAT	2	0.39407407	0.19703704	.	.
AREA*HABITAT	4	3.53037037	0.88259259	.	.
REP(AREA*HABITAT)	18	10.23333333	0.56851852	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	5.75629630	2.87814815	5.06	0.0180**
HABITAT	2	0.39407407	0.19703704	0.35	0.7117
AREA*HABITAT	4	3.53037037	0.88259259	1.55	0.2297

Dependent Variable: STONE

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	11.80962963	0.45421652	.	.
Error	0	.	.		

Corrected Total	26	11.80962963

R-Square	C.V.	Root MSE	STONE Mean
1.000000	0	0	0.50370370

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	1.00074074	0.50037037	.	.
HABITAT	2	1.86740741	0.93370370	.	.
AREA*HABITAT	4	4.11481481	1.02870370	.	.
REP(AREA*HABITAT)	18	4.82666667	0.26814815	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	1.00074074	0.50037037	1.87	0.1835
HABITAT	2	1.86740741	0.93370370	3.48	0.0527*
AREA*HABITAT	4	4.11481481	1.02870370	3.84	0.0200**

Dependent Variable: MOSS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	5065.38296296	194.82242165	.	.

Error	0	.	.		
Corrected Total	26	5065.38296296			

R-Square	C.V.	Root MSE	MOSS Mean
1.000000	0	0	11.63703704

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	40.71407407	20.35703704	.	.
HABITAT	2	4281.16962963	2140.58481481	.	.
AREA*HABITAT	4	33.73925926	8.43481481	.	.
REP(AREA*HABITAT)	18	709.76000000	39.43111111	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	40.71407407	20.35703704	0.52	0.6053
HABITAT	2	4281.16962963	2140.58481481	54.29	0.0001***
AREA*HABITAT	4	33.73925926	8.43481481	0.21	0.9273

Dependent Variable: LICHEN

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	26	222.94740741	8.57490028	.	.
Error	0	.	.		

Corrected Total	26	222.94740741	

R-Square	C.V.	Root MSE	LICHEN Mean
1.000000	0	0	2.44814815

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	11.65851852	5.82925926	.	.
HABITAT	2	104.13851852	52.06925926	.	.
AREA*HABITAT	4	25.63037037	6.40759259	.	.
REP(AREA*HABITAT)	18	81.52000000	4.52888889	.	.

Tests of Hypotheses using the Anova MS for REP(AREA*HABITAT) as an error term

Source	DF	Anova SS	Mean Square	F Value	Pr > F
AREA	2	11.65851852	5.82925926	1.29	0.3003
HABITAT	2	104.13851852	52.06925926	11.50	0.0006***
AREA*HABITAT	4	25.63037037	6.40759259	1.41	0.2692

* p<0.1, ** p<0.05, *** p<0.01

Appendix 9: Multiple comparison of least square means for ground cover between habitats and study areas.

General Linear Models Procedure
Least Squares Means

Standard Errors and Probabilities calculated using the Type III MS for REP(AREA*HABITAT) as an error term

AREA	GRASS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	54.7777778	3.2628347	0.0001	1	.	0.0380**	0.0075***
GRS	65.1111111	3.2628347	0.0001	2	0.0380**	.	0.4510
ONFR	68.6666667	3.2628347	0.0001	3	0.0075***	0.4510	.

AREA	FORB LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	1.84444444	0.64146822	0.0101	1	.	0.0417**	0.3521
GRS	3.83333333	0.64146822	0.0001	2	0.0417**	.	0.2320
ONFR	2.71111111	0.64146822	0.0005	3	0.3521	0.2320	.

AREA	SHRUB LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	14.0000000	1.5542322	0.0001	1	.	0.0234**	0.0528*
GRS	8.5555556	1.5542322	0.0001	2	0.0234**	.	0.6907
ONFR	9.4444444	1.5542322	0.0001	3	0.0528*	0.6907	.

AREA	CACTI LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	1.33333333	0.32075015	0.0006	1	.	0.0248**	0.0248**
GRS	0.22222222	0.32075015	0.4973	2	0.0248**	.	1.0000
ONFR	0.22222222	0.32075015	0.4973	3	0.0248**	1.0000	.

AREA	GRND LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	11.1111111	1.3522272	0.0001	1	.	0.0110**	0.0111**
GRS	5.6888889	1.3522272	0.0005	2	0.0110**	.	0.9954
ONFR	5.7000000	1.3522272	0.0005	3	0.0111**	0.9954	.

AREA	DUNG LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	1.51111111	0.25133389	0.0001	1	.	0.0421**	0.0063***
GRS	0.73333333	0.25133389	0.0092	2	0.0421**	.	0.3766
ONFR	0.41111111	0.25133389	0.1193	3	0.0063***	0.3766	.

AREA	STONE LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	0.66666667	0.17261008	0.0011	1	.	0.8225	0.0928*
GRS	0.61111111	0.17261008	0.0023	2	0.8225	.	0.1391
ONFR	0.23333333	0.17261008	0.1932	3	0.0928*	0.1391	.

AREA	MOSS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	11.1111111	2.0931399	0.0001	1	.	0.4625	0.8301
GRS	13.3333333	2.0931399	0.0001	2	0.4625	.	0.3457
ONFR	10.4666667	2.0931399	0.0001	3	0.8301	0.3457	.

AREA	LICHEN LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	3.36666667	0.70937288	0.0002	1	.	0.2268	0.1522
GRS	2.11111111	0.70937288	0.0081	2	0.2268	.	0.8102
ONFR	1.86666667	0.70937288	0.0169	3	0.1522	0.8102	.

HABITAT	GRASS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	71.7777778	3.2628347	0.0001	1	.	0.7759	0.0001***
RD	70.4444444	3.2628347	0.0001	2	0.7759	.	0.0001***
UPLD	46.3333333	3.2628347	0.0001	3	0.0001***	0.0001***	.

HABITAT	FORB LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	4.25555556	0.64146822	0.0001	1	.	0.0598*	0.0114**
RD	2.43333333	0.64146822	0.0013	2	0.0598*	.	0.4294
UPLD	1.70000000	0.64146822	0.0163	3	0.0114**	0.4294	.

HABITAT	SHRUB LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	15.8888889	1.5542322	0.0001	1	.	0.0013***	0.0037***
RD	7.5555556	1.5542322	0.0001	2	0.0013***	.	0.6546
UPLD	8.5555556	1.5542322	0.0001	3	0.0037***	0.6546	.

HABITAT	CACTI LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	0.11111111	0.32075015	0.7331	1	.	0.1589	0.1036
RD	0.77777778	0.32075015	0.0261	2	0.1589	.	0.8093
UPLD	0.88888889	0.32075015	0.0126	3	0.1036	0.8093	.

HABITAT	GRND LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	3.5888889	1.3522272	0.0161	1	.	0.0001***	0.2403
RD	13.0000000	1.3522272	0.0001	2	0.0001***	.	0.0016***
UPLD	5.9111111	1.3522272	0.0004	3	0.2403	0.0016***	.

HABITAT	DUNG LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	1.05555556	0.25133389	0.0005	1	.	0.4628	0.5004
RD	0.78888889	0.25133389	0.0057	2	0.4628	.	0.9508
UPLD	0.81111111	0.25133389	0.0047	3	0.5004	0.9508	.

HABITAT	STONE LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	0.14444444	0.17261008	0.4137	1	.	0.0784*	0.0201**
RD	0.60000000	0.17261008	0.0027	2	0.0784*	.	0.5035
UPLD	0.76666667	0.17261008	0.0003	3	0.0201**	0.5035	.

HABITAT	MOSS LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	2.6111111	2.0931399	0.2282	1	.	0.9351	0.0001***
RD	2.8555556	2.0931399	0.1893	2	0.9351	.	0.0001***
UPLD	29.4444444	2.0931399	0.0001	3	0.0001***	0.0001***	.

HABITAT	LICHEN LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	0.43333333	0.70937288	0.5489	1	.	0.1899	0.0002***
RD	1.80000000	0.70937288	0.0206	2	0.1899	.	0.0040***
UPLD	5.11111111	0.70937288	0.0001	3	0.0002***	0.0040***	.

* p<0.1, ** p<0.05, *** p<0.01

Study Areas:

BRD=Border
GRS=Grasslands
ONFR=Onefour

Habitats:

CUL=Coulee
RD=Roadside
UPLD=Upland

Appendix 10: Multiple comparison of least square means for snow depth (cm) between study areas, habitats, and winter periods.

General Linear Models Procedure
Least Squares Means

Standard Errors and Probabilities calculated using the Type III MS for REP(AREA*HABITAT) as an error term

AREA	SNOW LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
BRD	15.8312037	0.5675211	0.0001	1	.	0.0468**	0.0001***
GRS	13.9237037	0.7640487	0.0001	2	0.0468**	.	0.0001***
ONFR	8.7803704	0.4633790	0.0001	3	0.0001***	0.0001***	.

HABITAT	SNOW LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
CUL	14.5514259	0.5103685	0.0001	1	.	0.7108	0.0001***
RD	14.1940926	0.8073197	0.0001	2	0.7108	.	0.0002***
UPLD	9.7897593	0.5103685	0.0001	3	0.0001***	0.0002***	.

WINTER	SNOW LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	Pr > |T| H0: LSMEAN(i)=LSMEAN(j) i/j	1	2	3
EAR	4.1380185	0.7426724	0.0001	1	.	0.0116**	0.0001***
LATE	6.5962963	0.4633790	0.0001	2	0.0116**	.	0.0001***
MID	27.8009630	0.6715000	0.0001	3	0.0001***	0.0001***	.

* p<0.1, ** p<0.05, *** p<0.01

Study Areas:
BRD=Border
GRS=Grasslands
ONFR=Onefour

Habitats:
CUL=Coulee
RD=Roadside
UPLD=Upland

Winter Session:
EAR=early winter
LATE=late winter
MID=mid winter